University of Alberta

Coralline algae as habitat for marine invertebrates on rocky coasts near Bamfield, British Columbia

by

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ABSTRACT

Abundance and distribution of epibiotic meiofauna and macrofauna were characterized for both intertidal and subtidal samples of articulated coralline algae (Rhodophyta: Rhodophyceae) at three sites in Barkley Sound, British Columbia, Canada. Intertidal samples were taken from transects located in low and high intertidal zones, both when these transects were exposed at low tide and when submerged at high tide. Overall, there was no difference in invertebrate assemblages from the low and high transects but there was a difference between samples taken when submerged and exposed. Multivariate regression trees correlating environmental variables to assemblage structure identified the presence of branching bryozoans and hydroids as being most influential in both the intertidal and the subtidal samples. Presence of these sessile organisms was associated with increased abundance of most motile organisms. This suggests that these branching organisms increase habitat complexity or act as food for associated invertebrates.

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CHAPTER 1: INTRODUCTION

Species diversity has long been hypothesized as being important for ecosystem functioning (Hacker and Gaines 1997). Losses in species diversity may result in decreased productivity (Naeem et al. 1994), increased invasion success (Stachowicz et al. 1999), and decreases in ability to buffer natural variation (Chapin et al. 1998). Loss of biodiversity in the marine environment has been associated with decreases in population recovery potential after perturbation and with changes in water quality (Worm et al. 2006). One goal of ecology is to understand the determinants of local species richness and the factors that influence patterns of species distributions within and among potential habitats (Connell 1972, Underwood 1981, Dean and Connell 1987).

The mechanisms that determine local diversity include biological, chemical, and physical factors. Traditionally, ecologists have focused on negative biological interactions such as competition and predation as regulators of species diversity (Menge 1976). Only relatively recently have positive interactions affecting species richness been investigated (Hacker and Gaines 1997, Stachowicz 2001). Positive interactions include mutualisms and commensalisms where at least one species benefits from the association with no negative impact suffered by either party (Hacker and Gaines 1997). Habitat complexity also can increase species diversity (Hicks 1980, Dean and Connell 1987, Hall and Bell 1988). Some species also can create habitats through their activities or physically act as habitats for other organisms (e.g., plants, coral), and their abundance can affect species richness of a given area.

Foundation Species as Ecosystem Engineers

'Ecosystem engineers' are organisms that physically modify their environment in some way that alters the availability of resources for other organisms, but not through a trophic interaction (Jones et al. 1994). Engineers can be defined as being either allogenic (changing living and non-living habitats from one state to another through their activities, e.g. beavers or termites) or autogenic (modifying the environment by their own physical presence, e.g. trees or corals) (Jones et al. 1994). Autogenic engineers are also termed 'facilitator species' (Stachowicz 2001) or 'foundation species' (Dayton 1972). Foundation species modify the environment by adding their physical structure as habitat for other organisms and increase the species richness of an area (Bruno and Bertness 2001). Specifically, foundation species "...alter local environmental conditions, often making a stressful habitat more hospitable for other individuals or species" (Stachowicz 2001). Understanding how foundation organisms increase species diversity can have conservation implications (Stachowicz 2001). Hacker and Gaines (1997) suggest that foundation species also could be termed 'keystone species' because of the large impact that these ecosystem engineers can have. Other ecologists would likely disagree with this argument, however, given that this term is typically reserved for top trophic-level organisms, and to those whose impact far outweighs their biomass (Power and Mills 1995).

Foundation species are 0thought to be most influential in harsh environments (Jones et al. 1997, Stachowicz 2001) and are found in both terrestrial and aquatic ecosystems. Marine invertebrates such as corals (Wood 1995, McClanahan 2007), oysters (Castel et al. 1989, Monteforte and Garcia-Gasca 1994), and barnacles (Harley

2006) act as foundation species and shelter a variety of fauna that otherwise would not find purchase in wave-swept areas. Autotrophic marine species including mangroves (Ellison et al. 1996, Chinnadurai and Fernando 2007), seagrasses (Schneider and Mann 1991), and intertidal algae (Bates 2007) are commonly considered foundation species, and their influence on community structure has been studied widely. Foundation species are so important that marine benthic communities are thought to rely on these habitat-forming species (Bruno and Bertness 2001).

Marine foundation species alter the habitat in a number of ways. Seagrasses and some algae grow vertically into the water column and alter flow patterns and thereby sediment deposition rates (Eckman et al. 1989). *Spartina alterniflora*, an intertidal salt marsh grass, stabilizes substrate by attenuating wave action (Bruno 2000). Foundation species also provide refuge from predators (Woodin 1978). Perhaps one of the best-studied foundation algal species and their associated fauna in the marine environment are giant forest forming kelps which provide refuge for juvenile fish as well as ameliorating environmental factors (Graham 2004).

The Role of Habitat Complexity in Increasing Species Diversity

The degree to which foundation organisms increase species diversity can be affected by factors such as their own morphological complexity. Increases in habitat complexity have been associated with increases in species diversity (Hicks 1980, Gee and Warwick 1994). This relationship, first hypothesized by MacArthur and MacArthur (1961), has been observationally and experimentally tested in a variety of habitats, both terrestrial and aquatic. There are several ways in which increased habitat complexity is though to increase species richness and abundance. It can provide protection from

predators (Heck and Wetstone 1977, Coull and Wells 1983), greater habitable space (Heck and Wetstone 1977), protection from desiccation, wave action, and other disturbances (Dommasnes 1968, Woodin 1978), increased food availability (Hicks 1980), and increased sediment loading which provides habitat for interstitial animals (Hicks 1980, Gibbons 1988).

Quantification of habitat complexity for algal foundation species has been measured using a variety of methods including weight of epiphytes (Hall and Bell 1988), fractal dimensions of the algae (Gee and Warwick 1994), and frond length (Kelaher 2003). Through the course of my study, the dry weight of algae and associated sessile epifauna (e.g. bryozoans and sponges) are considered as the measures of increased habitat complexity for motile fauna.

Several studies have compared the role of habitat complexity in influencing local species richness with those of other hypothetically important factors. In benthic freshwater systems, habitat complexity has a greater effect on species diversity than does seasonality (Melo and Froehlich 2001). Beck (2000) separated structural components from complexity and found that increased complexity has positive effects on distributions of marine gastropods. Schmude et al. (1998) experimentally found that macroinvertebrates in temperate lakes were more diverse and abundant on complex artificial substrates than on simple artificial substrates. The effect of habitat complexity has been well studied in marine intertidal algae. Many researchers have compared the complexity of different algal species and have found increases in density, abundance, or diversity of the associated epifauna with increasing complexity (Hicks 1980, Dean and

Connell 1987, Gee and Warwick 1994, Hull 1997, Hooper and Davenport 2006, Frame et al. 2007).

Coralline Algae as a Foundation Species

Coralline algae (Rhodophyta: Rhodophyceae) are diverse and widespread marine autotrophs. There are currently 34 species in 16 recognized genera in the family Corallinacea off the coast of British Columbia, Washington, and Oregon (Gabrielson et al. 2000). Geniculate coralline algae that form intertidal turfs host a variety of associated motile and sessile fauna (Hicks 1971, Stewart 1982, Kelaher et al. 2001, Chapman et al. 2005). These turfs display high habitat heterogeneity (Hicks 1980) due to the combination of the branched habit of the algae and the sessile epifauna and epiphytes growing directly on the alga. Coralline algae can potentially mitigate both physical stresses (decreasing desiccation and wave force) and biotic stresses (providing refuge from predators and increased niches to reduce competition). Davenport et al (1999) found *Corallina* sp. to have a greater fractal dimension (habitat complexity) than brown algae *Hormosira banksii* (Turner) and green algae *Enteromorpha* sp., and observed greater abundance, biomass, and taxon richness of associated epifauna on the coralline alga.

Although coralline algal turfs are distributed world-wide on rocky shores, organisms associated with this complex algae have been rarely studied. The majority of the research on associated fauna is from Australia and New Zealand (Hicks 1971, Coull and Wells 1983, Taylor 1998, Brown and Taylor 1999, Davenport et al. 1999, Kelaher et al. 2001, Chapman et al. 2005). Other studies have examined epifauna from Japan (Akioka et al. 1999), western Europe (Dommasnes 1968, 1969, Grahame and Hanna

1989, Hull 1997, Kelaher et al. 2004), the Mediterranean (Ballesteros 1988), and Chile (López and Stotz 1997, Kelaher et al. 2004). The few studies that have looked at these assemblages from the Pacific ocean of North America were situated in southern California. Two of the three focused on ostracod assemblages (Frame et al. 2007, Huff and Jarett 2007) and the other on algal epiphytes (Stewart 1982). No previous studies have been conducted off the west coast of British Columbia where rocky shores dominate the coastline.

Coralline algae may act directly as a foundation species, or indirectly by providing substrate for other attached organisms that themselves act as habitat. Sessile epifauna in the form of bryozoans, sponges, and colonial hydrozoans are known to grow on the algae (Hicks 1971, Chapman et al. 2005, Kelaher and Castilla 2005). Presence of upright sessile epifauna on shell-covered seabed (Bradshaw et al. 2003) and epiphyte biomass on two intertidal seaweeds, *Ascophyllum nodosum* and *Fucus vesiculosus* (Johnson and Scheibling 1987), have been found to increase overall epibiotic diversity and abundance. To my knowledge, no studies have attempted to assess the impacts sessile animals may impose on motile fauna associated with geniculate coralline algae.

Determining patterns in abundance and diversity of organisms that inhabit coralline algae can further our understanding of how foundation species alter the environment and the degree to which habitat complexity can affect species diversity. The epifauna living on coralline algae are prey for higher trophic groups such as fish (Coull and Wells 1983), and so understanding their distribution may provide explanation for foraging strategies of highly mobile predators.

Study objectives

The objectives of this study are three-fold. First, I identify and quantify fauna living on turf-forming intertidal and subtidal coralline algae off the west coast of Vancouver Island. Second, I determine whether various abiotic factors such as tidal height and exposure at the time of sampling affect the diversity and abundance of invertebrates observed. And third, I examine whether the presence of sessile epifaunal invertebrates (bryozoans, sponges, and colonial hydroids) alter diversity and abundance of other animals in coralline algae.

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CHAPTER 2: SURVEY OF THE INVERTEBRATE ASSEMBLAGES ASSOCIATED WITH SUBTIDAL CORALLINE ALGAE IN BARKLEY SOUND, BRITISH COLUMBIA

INTRODUCTION

The shallow rocky subtidal zone is home to a wide diversity of marine organisms. Thought to be more biologically diverse than its near-shore counterpart, the rocky intertidal, the shallow rocky subtidal is a physically moderately stressful habitat without the desiccation stress that affects the intertidal zone (Osman and Whitlatch 1998). Despite this obvious difference between the two habitats, much of what is published about subtidal ecology is based on the more easily accessible intertidal zone (Dayton 1971). Species distributions in subtidal settings are controlled by some similar factors as the rocky intertidal including interspecific competition, predation, and disturbances (Connell 1972, Menge and Sutherland 1976), but are also greatly affected by competition for space, larval recruitment, light, depth, turbidity, and siltation (Sebens 1986, Wood 1987, Smith and Witman 1999). Competition for space is thought to be more important for species distributions on small spatial scales (Sebens 1986), such as those examined in this study.

The subtidal zone is filled with sessile organisms that provide habitat for other organisms ('foundation species' (*sensu* Dayton 1972)). Because space is such a limiting factor in the subtidal zone (Sebens 1986), any solid substratum available, be it mineral or organic, is utilized. Although macroalgae (e.g. kelps) and colonial animals (e.g. ascidians and bryozoans) dominate the rocky subtidal (Butler 1995), smaller turf- forming algae are also present (Wood 1987). These habitat forming organisms vary in their complexity, with many of the larger flat-fronded macroalgae being structurally simple when

compared to smaller, more finely branched species such as geniculate coralline algae (Taylor 1998).

The small-bodied animals that utilize the habitat provided by macroalgae, colonial animals, and turf forming algae are an important food source for a variety of larger animals. Juvenile flatfish (Hicks 1984) and chum salmon (Sibert et al. 1977) feed on harpacticoid copepods. Because of their high densities and rapid rate of turnover, such meiofauna are relatively productive compared to other rocky shore dwelling animals (Taylor 1998). Considering their potential ecological importance, knowledge of epifaunal organisms inhabiting subtidal algae is lacking.

Along with a variety of motile epifauna, sessile invertebrates and other algae also use foundation algae as habitat on which to settle. These sessile epibiota can also act as substrate for other organisms, thereby increasing the overall complexity of the initial foundation organism. Both algal epiphytes and colonial hydroids have been shown to increase species richness of associated meiofauna (Hall and Bell 1988, Bradshaw et al. 2003). There are several ways in which these organisms could increase species abundance and diversity: expanding habitable space, providing refuge from predators, providing sites for food (detritus) accumulation, and acting as a food source themselves.

Coralline algae (Rhodophyta: Rhodophyceae), both geniculate and encrusting, are common elements of the subtidal community. Coralline algae are comparatively resilient to herbivory because of their calcium-carbonate skeleton (Padilla 1984). The complex branching patterns observed in geniculate algae provide habitat for a variety of organisms. Most studies of epiphytes on coralline algae are from intertidal studies.

Epifauna of subtidal coralline algae has been studied once in New Zealand by Taylor (1998), who didn't give a full description of the epifaunal community, and generally looked at organisms to class. Taylor (1998) found densities of up to 159 006 organisms m^{-2} inhabiting these subtidal coralline turfs. To my knowledge, no studies have been conducted off the coast of British Columbia. In this study I sought to characterize the assemblage of invertebrates living on patches of subtidal *Corallina officinalis* Linnaeus, *C. vancouveriensis* Yendo, and *Bossiella* spp., and to determine if the presence of sessile epifauna (bryozoans, colonial hydrozoans, and sponges) had any impact on overall assemblage structure.

METHODS

Study Location

This study was conducted at the Bamfield Marine Sciences Centre in Barkley Sound, British Columbia, Canada (latitude 48°50.08' N, longitude 125°08.8'W). Three sites were sampled: Aguilar Point, Scott's Bay, and Dixon Island (Fig. 2-1). All shores are near vertical walls of shallow rocky subtidal habitat representative of Barkley Sound. Aguilar Point and Scott's Bay face northwest and Dixon Island faces southwest. At all three sites tufts of coralline algae, *Corallina officinalis* and *Bossiella* spp. are interspersed within the *Laminaria* spp. bed.

Field Sampling

Subtidal algal sampling took place from 2 December 2005 to 8 December 2005 via SCUBA diving. Sampling dates were chosen based on minimized ocean swell for safety reasons. Sampling occurred from the deepest boundary of the geniculate coralline algal zone and was sampled ascending vertically until it was no longer safe for the divers

to sample due to swell and waves. A total of 44 samples (15 each from Aguilar Point and Scott's Bay, and 14 from Dixon Island) were taken by removing tufts of algae from the rock face by hand and placing them into individual whirl packs. All samples were immediately returned to the lab for processing.

Laboratory Analysis

All samples were brought back to the lab, sieved through a 53-µm mesh, and fixed in a 4% Formalin solution. Samples were later transferred into 80% ETOH and stained with a Rose Bengal solution, a stain that binds to proteins making pale organisms more visible again a light background.

All 44 samples were examined under 25X stereomicroscopes (Leica MZ 16 and Zeiss Stemi1000) for identifiable invertebrates (head must be present to be counted) by filling a gridded Petri dish with the sample and systematically working through the dish. All clumps of algae were also sorted through to remove animals attached to the fronds. All solitary invertebrates found were counted and identified to the following taxonomic levels: Nematoda, Entoprocta, and Nemertea to phylum; Mollusca, Platyhelminthes, Porifera and Echinodermata to class. Depending on the difficulty of identification, annelids were identified to either family or class and arthropods were identified to class, order, suborder or family (see Appendix 1 for details and level of taxonomic resolution). Ectoprocts (hereafter called bryozoans) were identified to order and cnidarians to class except one group which was identified to genus. Identifications were done on the Leica MZ 16 from 25X magnification to 115X using Light's Manual (Smith and Carlton 1975) and Kozloff's Manual (Kozloff 1999).

The coralline algae from all the sorted samples was separated and identified to genus or species, and any easily visible sessile invertebrates, epiphytes and fouling agents were removed. The algae were then dried in a 60°C drying oven for 24 hours and weighed on Whatman filter paper (42, ashless circles, 90 mm diameter). Though not tested for, dry weight of algae is assumed to be representative of surface area of the algae. Algae was identified to genus for *Bossiella* spp. and species for *Corallina* spp.. To account for other sources of biogenic habitat in the samples, bryozoans and colonial hydrozoans (*Aglaophenia* spp.) were removed from the coralline algae, placed onto Whatman filter paper dried in a 60°C oven for 24 hours and weighed. Sponges, solitary hydrozoans, anthozoans, and entoprocts were all characterized as either present or absent in the samples.

Fifteen of the 44 samples had a large number of nematodes present and therefore required subsampling (see nematode subsampling section below).

Nematode Subsampling

Subsampling occurred once all coralline algae had been removed, as had all other animals except nematodes. 80% ethanol was added to the sample to make the total volume 125 mL. The sample was then stirred to suspend the animals and 9 mL were removed via pipette and placed into a Petri dish with a grid on the bottom. All nematodes were then counted in the dish and returned to the initial sample, which was then topped back up to 125 mL if necessary. This process was completed 5 times for each sample and an average number of nematodes per sample was calculated. This average was then multiplied by 13.9 and used as the number of nematodes per sample.

Data Analysis

All data were organized using Microsoft Excel 2004 for Mac (version 11.3.5). Several statistical packages were used for analysis of data. Univariate data were analyzed using SPSS 13 for Mac OS X (version 13.0.0). Multivariate data were analyzed using PATN (version 3.03) (Belbin 1989) and R (version 2.5.1 GUI 1.20) (R Development Core Team 2005).

To determine if there was an effect of biomass of algae in a sample on number and diversity of animals, regressions of the total number of individuals/gram of dry algae per sample and total number of taxa/ gram of dry algae per sample were performed. In both cases there were significant positive relationships (see Results for details of regression) (Fig. 2-2). Due to these significant results, all further analyses were done on data standardized per unit dry weight of algae. The abundance of each taxon was standardized to one gram of algae by dividing the count for each taxon by the weight (g) of coralline algae sampled (see Appendix 1 for initial and standardized values).

I analyzed the assemblages categorized by site (Aguilar Point, Scott's Bay, and Dixon Island) to determine in assemblage structure was similar with raw data using semi-strong hybrid multidimensional scaling (SSH-MDS) using Bray-Curtis distance measures and 1000 random starts to create the ordination. Only taxa present in 3 or more of the 44 samples were included in the analyses (see Appendix 1 for excluded taxa). The Bray-Curtis distance matrix was then analyzed with a multivariate analysis of similarity (ANOSIM) in PATN (Belbin 1989) with 1000 permutations to identify if the assemblage structure varied significantly among the three sites. ANOSIM calculates a p-value from a

randomized distribution. A Monte-Carlo Attributes in Ordination (MCAO) and a Principal Component Correlation (PCC) was also run to determine important vectors.

An indicator species analysis (Dufrene and Legendre 1997) was run to determine taxa indicative of the three sites using the duleg function in the labdsv library with 1000 iterations in R to detect possible associations between invertebrate taxa identified and each of the sites. Since I used higher taxonomic ranks I will be calling this an 'indicator taxon analysis' (ITA) from now on. Indicator taxon analyses in R (R Development Core Team 2005) provide a p-value as well as an indicator value (IV), which ranges from 0 (no indication) to 1 (perfect indication); values greater than 0.6 are generally considered good indicators (Jacobs et al. 2007).

A multivariate regression tree (MRT) was used to identify which environmental factors (site, the weight of erect bryozoans, encrusting bryozoans, *Flustrellidra* spp., and *Aglaophenia* spp.) split the assemblage data in a way that minimizes dissimilarity within clusters (De'Ath 2002). The MRT was run using the R package (R Development Core Team 2005) and mvpart library (Therneau and Atkinson 2005) with a Bray-Curtis distance matrix. The MRT analysis was run 100 times and the most common tree was selected. Trees are composed of terminal nodes (final groups) and higher nodes (where splitting occurs). MRT also provides a measure of residual error, standard error, and cross-validated error. The cross-validated error is a measure of predictability of the tree and ranges from 0 (perfect prediction) to 1 (no prediction), but can range greater than 1 in some cases. The best tree is the tree with the lowest cross-validated error, and therefore greatest predictability power (De'Ath 2002). Follow up ITAs were done for each higher node produced by the tree. For each taxon indicated as significant by the ITA for the first

higher node, a post-hoc t-test or Mann-Whitney test was done to determine where the significant difference lay. No post-hoc tests were done for the second or third higher nodes because of low sample sizes (see results for details).

All figures were made with SIGMAPLOT 13.0 for PC.

RESULTS

Invertebrates Found in Subtidal Samples

A total of 35 990 invertebrates from 11 phyla were found in samples and were identified to 38 taxonomic groups (Table 2-1 and see Appendix 1 for details). Of the phyla, Arthropoda had the greatest number of individuals, and Harpacticoida (harpacticod copepods) was the most abundant of the 38 taxonomic groups overall. Nematodes represented the second most abundant phylum followed by the annelids and then molluscs.

Relationship between taxon richness, total individuals and algal weight

There was a significant positive relationship between the dry weight (g) of algae collected for the samples and associated taxon richness (Regression: $p=0.002$, $R^2=0.21$) (Fig. 2-2). There was also a significant positive relationship between weight of algae and total number of individuals per sample (Regression: $p=0.027$, $R^2=0.11$) (Fig. 2-2).

Effect of Site

A total of 8937 individuals from 33 taxa were found in Aguilar Point samples, 9963 individuals from 32 taxa in Dixon Island samples, and 17090 individuals from 35 taxa from Scott's Bay samples. Most algae collected from Aguilar Point was identified as *Bossiella* spp., and Dixon Island samples were predominantly *Corallina officinalis*, while Scott's Bay was a mixture of these two (see Appendix 1). ANOSIM found a

significant difference in assemblage structure between samples from Aguilar Point and those from Scott's Bay (ANOSIM: $p=0.001$) and from Dixon Island (ANOSIM: $p=0.029$); however, there was no significant assemblage difference between samples taken at Scott's Bay and Dixon Island (ANOSIM: $p=0.078$) (Fig. 2-3). Post-hoc univariate analyses showed that Scott's Bay had significantly more invertebrates per sample than did Aguilar Point (Fig. 2-4). There was no difference in mean taxon richness per sample among the three sites (Fig. 2-4).

PCC and MCAO revealed that significant intrinsic vectors included halacarid mites, syllid and polynoid polychaetes, ostracods, gastropods, janirid isopods, nematodes, and total individuals per sample (Fig. 2-4). All vectors pointed toward samples from Scott's Bay indicating increased abundance of organisms at this site. An indicator taxon analysis found that 11 of the 33 taxa included in the matrix were important for differentiating the sites (Table 2-2); however two of those groups (nemerteans and jaeropsid isopods) had low indicator values ($IV<0.6$) and hereafter will not be considered as indicators. Nematodes, harpacticoid copepods, terebellid polychaetes, gammarid amphipods, bivalves, janirid isopods, halacarid mites, and gastropods were all more abundant in samples from Scott's Bay than from Aguilar Point (Fig. 2-5). Nudibranchs were far more abundant in samples from Dixon Island than from either of the other sites (Fig. 2-5). Eight taxa were more abundant in the Scott's Bay samples than samples taken from Dixon Island and Aguilar Point. Of those eight taxa, five show that Dixon Island and Aguilar Point have similar abundances and three show that Dixon Island and Scott's Bay have similar abundances.

Environmental Factors Correlated With Assemblage Structure (MRT)

The multivariate regression tree (MRT) was run with six environmental factors: dry weight of erect bryozoans, encrusting bryozoans, colonial hydrozoans (*Aglaophenia* sp.), and *Flustrellidra* spp., presence or absence of sponges, and identity of the three sites. The MRT produced a tree with four terminal nodes and three higher nodes (Fig. 2-6). The dominant characteristic for dividing the invertebrate assemblage was the dry weight of erect bryozoans present (Fig. 2-6) which separated the assemblages into two groups. The first group (29 samples) had greater than or equal to 0.027 g erect bryozoans per sample and the second group (15 samples) had less than 0.027 g erect bryozoans per sample (Fig. 2-6). These two groups were also subdivided. Higher node two was split again by the weight of erect bryozoans, and higher node three was split by the weight of *Aglaophenia sp.*

An indicator analysis of higher node one identified five taxa as indicators of sample with greater masses of erect bryozoans (Table 2-3). High numbers of gastropods, gammarid amphipods, polynoid polychaetes, and jaeropsid isopods were associated with greater dry mass of erect bryozoans, while nereid polychaetes were significantly more abundant with lower masses of erect bryozoans (Fig. 2-7). Though significantly different between the two clusters, polynoid polychaetes and jaeropsid isopods each had a low indicator value (IV) < 0.3.

Indicator analysis of higher node two found 13 significant taxa (Table 2-4). Though I could not run t-tests or Mann-Whitney U tests because of the small sample size of terminal node two (n=3) the indicator analysis showed that paratanaid tanaids, terebellid, polynoid, and syllid polychaetes, as well as bivalves, entoprocts, nematodes,

halacarid mites, harpacticoid copepods, crabs, jaeropsid isopods, gastropods, and gammarid amphipods were more abundant in samples with the greatest amount of erect bryozoans. All taxonomic groups had relatively high indicator values ranging from 0.61-0.89.

Higher node three indicator analysis was split based on dry weight of the colonial hydroid *Aglaophenia* sp. and again found a greater abundance of organisms associated with a greater weight of the habitat modifier (Table 2-5). Again, post-hoc multiple comparisons could not be run because of the low sample size in terminal node 4 (n=2). This time, harpacticoid copepods, munnid and janairid isopods, nematodes, ostracods, syllid and sabellid polychaetes, nudibranchs, gastropods, caprellid amphipods, and halacarid mites responded most to the varied amount of the hydrozoan. All of these groups had high indicator values (IV>0.85) except sabellid polychaetes (IV=0.49).

DISCUSSION

Geniculate coralline algae acts as a foundation species for small-bodied marine invertebrates. Diversity of epifauna on subtidal coralline algae in Barkley Sound is similar to that of intertidal algae in New Zealand (Hicks 1971), with the minor exception that hemichordates and fish were found in New Zealand samples. In contrast, my results differed from what Taylor (1998) observed in New Zealand subtidal samples where gammarid amphipods followed by polychaetes were the most abundant taxa sampled, compared to my samples where harpacticoid copepods were the most abundant taxa followed by nematodes. As is quite common with species-area relationships (Hoyle 2004), I found a positive relationship between both taxon richness and abundance with increased amount of algae sampled (Fig. 2-2). However, based on sampling method, it is

impossible to determine if this is due to an increase in habitat complexity (Hoyle 2004) or solely due to the increase in overall surface area of algae. However, as will be discussed later, there are some suggestions that increases in habitat complexity may affect the invertebrate assemblages found.

Site

There was a significant difference in invertebrate assemblages between some of the sites sampled (Fig. 2-3). ANOSIM results indicate that samples from the Aguilar Point site were significantly different from the other two sites. This was surprising because geographically Scott's Bay and Dixon Island are the furthest apart with Aguilar in the middle (Fig. 2-1). Also, species of algal host did not influence invertebrate assemblage. Indicator taxon analysis identified several taxa as distinguishing the sites from one another. The majority of the taxa (nematodes, harpacticoid copepods, terebellid polychaetes, gammarid amphipods, bivalves, janirid isopods, halacarid mites, and gastropods) were most abundant at Scott's Bay but nudibranchs were most abundant at Dixon Island. The reasoning for these differences is unclear. Sites need to be reexamined and dominant algal cover, dominant macroinvertebrates found, slope, and other factors need to be considered to elucidate potential reasons for the observed differences.

Environmental Factors Correlated With Assemblage Structure (MRT)

MRT results suggest that although invertebrate assemblages are distinct between some of the sites, site is not necessarily the best indicator of how taxa are distributed. MRT identified weight of erect bryozoans and of the colonial hydroid *Aglaophenia sp.* as key differentiators of invertebrate assemblages. This is in agreement with Bradshaw et

al. (2003) who found that presence of colonial hydroids on shell-covered seabed greatly increased the abundance of motile epifauna in the Irish Sea. The majority of invertebrates identified as being indictor species of the three higher nodes of the MRT were significantly more abundant with the increased biomass of the sessile epifauna. There are several potential reasons for this. Bradshaw et al (2003) suggest that these branching sessile epibionts increase the complexity of the habitat, either by adding more surface area or by altering the way water flows through the algal turf. This extra structure could be collecting detritus and diatoms providing additional food for the associated motile fauna (Caine 1998). The sessile fauna may be using these branching organisms to move them higher into the water column away from the boundary layer to allow for increased rates of filter feeding (Bracken et al. 2007). Another possibility is that they are acting as a food source for the motile fauna present. Nudibranchs, known predators of hydrozoans (Caine 1998), were found in greater abundances on samples with a greater weight of the hydroid *Aglaophenia* sp. Syllid polychaetes, positively associated with both bryozoans and hydroids, are known to feed on both groups of colonial animals (reviewed in Fauchald and Jumars 1979).

Interestingly, nereid polychaetes were the only taxon to respond negatively to an increase in the epifauna on the coralline algae. Nereids were significantly more abundant in samples with lower biomass of erect bryozoans. It may be that the density of the epifauna hinders the feeding efficiency of these predatory polychaetes (Menge 1978).

And finally, it is possible that more complex biotic interactions may also be occurring within this algal-turf habitat. Caine (1998) observed a mutualistic relationship between a caprellid amphipod and a leptomedusan hydroid, the caprellid fending off

predatory nudibranchs in exchange for substrate and access to diatoms and detritus entrapped in the bryozoan.

CONCLUSIONS

Subtidal tufts of geniculate coralline algae host a great diversity of both motile and sessile invertebrates. Overall community composition resembles that of Hicks' (1971) intertidal samples from New Zealand. I also found the same classes of organisms that Taylor (1998) found in subtidal samples. Of the environmental factors measured, the most important in distinguishing assemblage structure were the abundance of erect bryozoans and colonial hydroids, which possibly add to the structural habitat complexity or food resources of the samples. In an analogous system, epiphytes on tropical rain-forest trees are known to house an increase diversity of associated arthropods (Stork 1987, Nadkarni 1994).

Despite the large area of coastal habitat that can be described as rocky subtidal, there is almost no published research on its ecology (Osman and Whitlatch 1998). The majority of papers focus on processes in seagrass beds and kelp forests, as they are usually easier to sample in. This paucity of data is likely due to the difficulty in sampling shallow subtidal rocky shores. Much of what ecologists assume about subtidal processes stem from observations made in adjacent intertidal zones. However, this information must be used cautiously as abiotic factors governing the two zones (though not necessarily the dominant factors) are quite different and may change both how species interact with each other and their spatial distribution.

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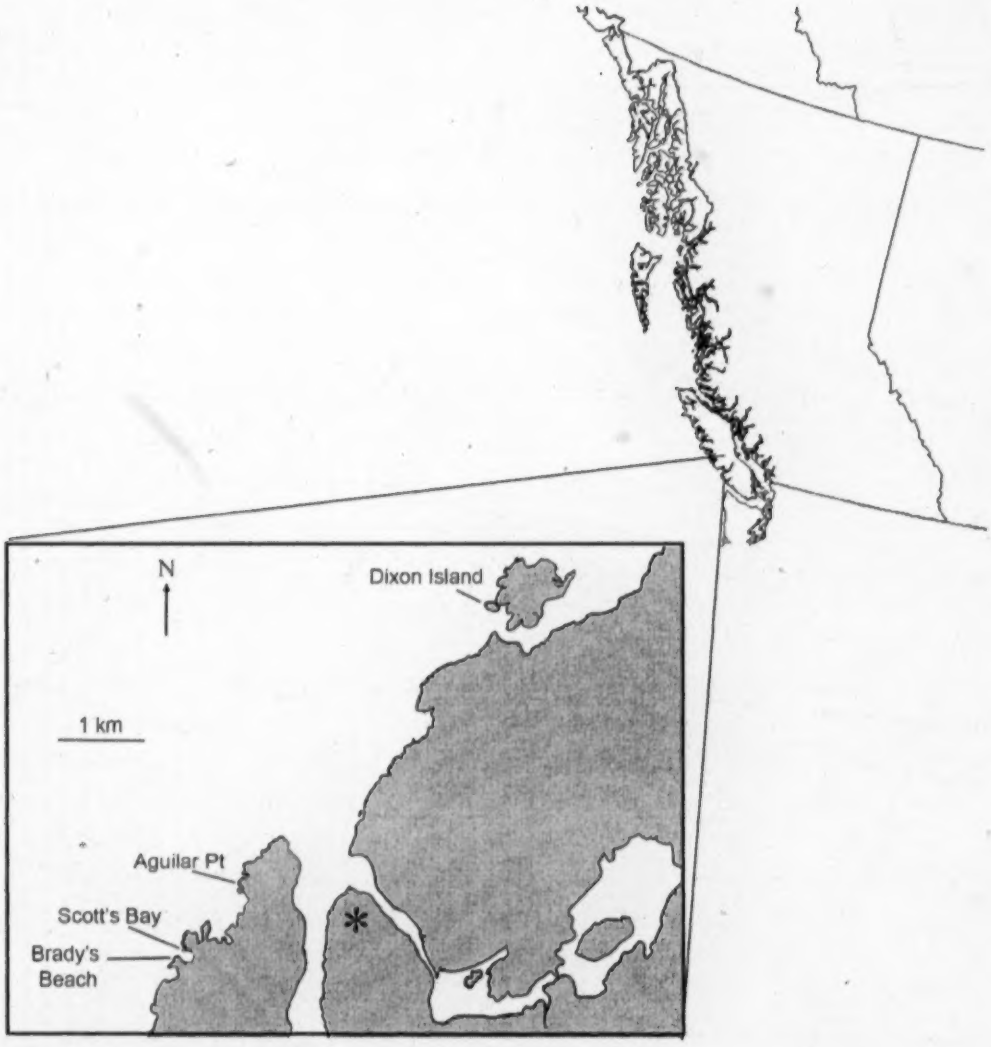

Figure 2-1: Map of Study Sites. Asterisk represents the Bamfield Marine Sciences Centre. Dixon Island, Aguilar Point, and Scott's Bay were used in the subtidal portion of the study. Aguilar Point, Scott's Bay, and Brady's Beach were sampled for the intertidal portion of the study.

Table 2-1: Taxa and number of individuals found in 44 subtidal samples.

Phylum	Lowest Taxonomic Ranking	Total Individuals	Percentage
Nematoda	Nematoda	8507	22.91%
Arthropoda	Harpacticoida	8488	22.86%
Arthropoda	Halacaridae	4081	10.99%
Arthropoda	Ostracoda	3798	10.23%
Arthropoda	Gammaridea	3440	9.26%
Annelida	Syllidae	2736	7.37%
Arthropoda	Caprellidea	1972	5.31%
Mollusca	Bivalvia	1633	4.40%
Mollusca	Gastropoda	648	1.74%
Arthropoda	Janaridae	439	1.18%
Annelida	Nereidae	381	1.03%
Nemertea	Nemertea	163	0.44%
Arthropoda	Munnidae	141	0.38%
Annelida	Terebellidae	120	0.32%
Mollusca	Nudibranchia	103	0.28%
Arthropoda	Jaeropsidae	91	0.25%
Annelida	Sabellidae	73	0.20%
Arthropoda	Paratanaidae	63	0.17%
Arthropoda	Sphaeromatidae	57	0.15%
Annelida	Polynoidae	53	0.14%
Annelida	Spirorbidae	26	0.07%
Annelida	Oligochaeta	23	0.06%
Platyhelminthes	Platyhelminthes	13	0.04%
Arthropoda	Cirripedia	12	0.03%
Arthropoda	Pycnogonida	10	0.03%
Arthropoda	Brachyura	9	0.02%
Echinodermata	Ophiuroidea	8	0.02%
Annelida	Phyllodocidae	7	0.02%
Arthropoda	Tanaidae	6	0.02%
Arthropoda	Anthuridae	4	0.01%
Arthropoda	Idoteidae	4	0.01%
Arthropoda	Calanoida	3	0.01%
Annelida	Spionidae	3	0.01%
Mollusca	Polyplacophora	1	0.00%
Annelida	Arabellidae	1	0.00%

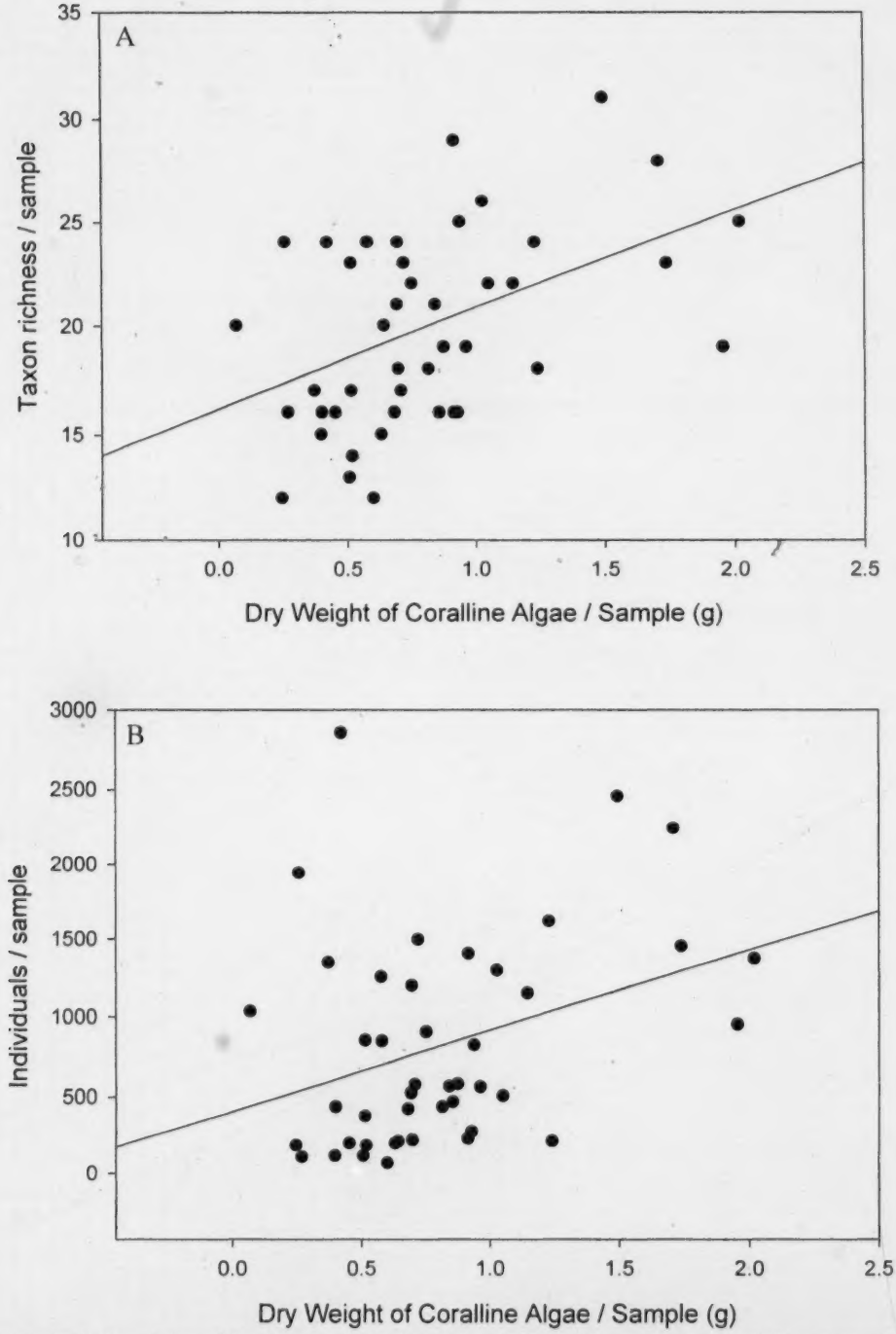

Fig 2-2: Relationship of invertebrate richness and abundance to dry weight of coralline algae per sample. A) Taxon richness (Regression: $p=0.002$, $R^2=0.21$). N=60 algal samples B) Total individuals (Regression: $p=0.027$, $R^2=0.11$). N=60 algal samples.

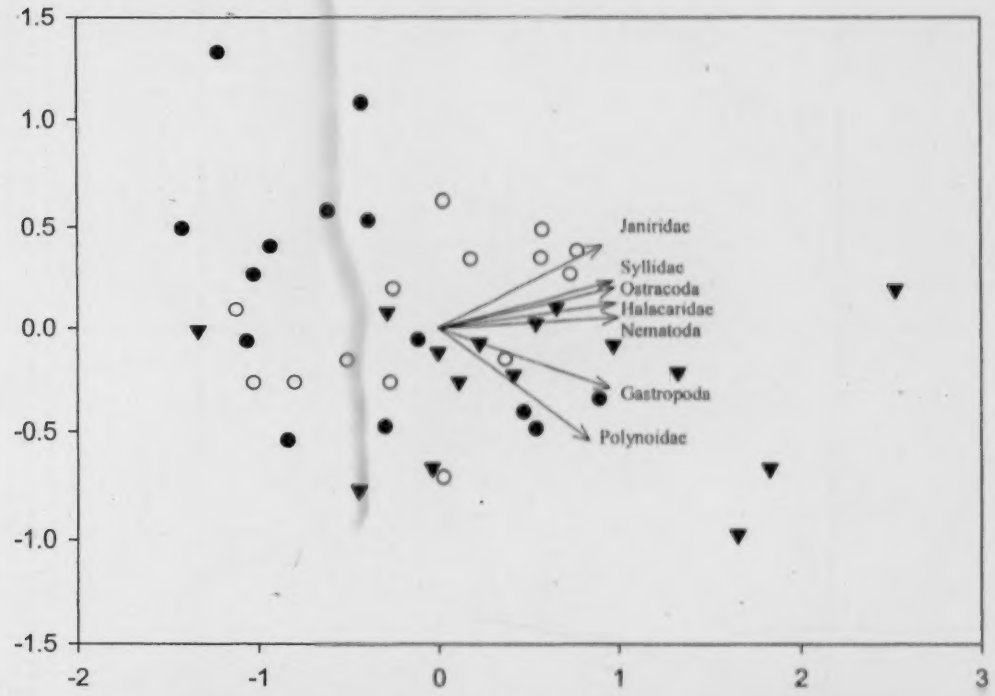

Fig 2-3: Two dimensional semi-strong hybrid multidimensional scaling (SSH-MDS) ordination comparing invertebrate assemblages at the three subtidal sites: Aguilar Point (closed circle n=15) Brady's Beach (open circle n=14) and Scott's Bay (triangle n=15). Nematodes are log 10 (x+1) transformed. SSH-MDS stress = 0.15. ANOSIM pairwise results. A/D=0.029 A/S=0.001, D/S=0.078.

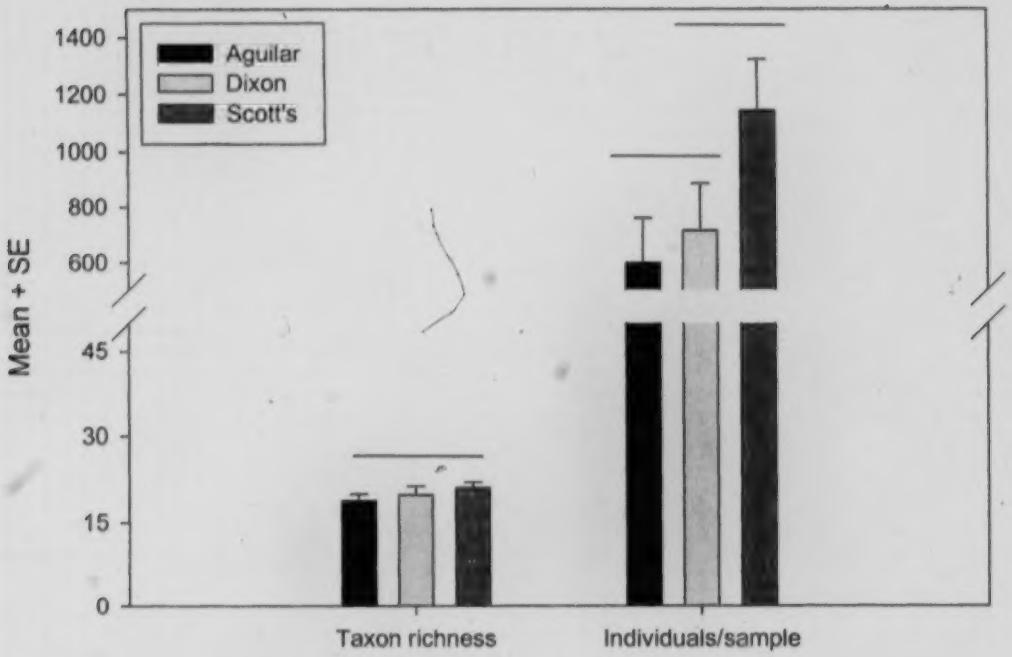

Fig 2-4: Comparison of three sites for mean taxon richness and mean individuals per sample. There are significantly more individuals per sample in Scott's Bay than in Aguilar Point (ANOVA p=0.002) but there is no significant difference in taxon richness between the three sites (ANOVA p=0.074). Lines indicate similarity. N=20 algal samples per site.

Table 2-2: Taxa identified by an indicator taxon analysis as being indicators of one of the three sites and subsequent post hoc test. Bold p-values indicate significance at level of $p<0.05$. Bold IV values show strong indicators at level of IV=0.5. Max class indicates the site with greatest abundance of the respective taxon.

	Indicator Taxon Analysis		**Post-hoc Univariate Test**		
Taxon	p-value	IV	Test	p-value	Max Class
Nematoda	**<0.001**	**0.73**	ANOVA	**<0.001**	Scott's
Nudibranchia	**0.002**	**0.59**	ANOVA	**0.002**	Dixon
Harpacticoida	**0.005**	**0.75**	ANOVA	**0.004**	Scott's
Terebellidae	**0.005**	**0.58**	Kruskall-Wallis	**0.007**	Scott's
Gammaridea	**0.007**	**0.72**	ANOVA	**0.004**	Scott's
Bivalvia	**0.019**	**0.61**	Kruskall-Wallis	**0.008**	Scott's
Janaridae	**0.020**	**0.62**	ANOVA	**0.005**	Scott's
Nemertea	**0.024**	0.43	ANOVA	0.054	Scott's
Halicaridae	**0.031**	**0.56**	ANOVA	**<0.001**	Scott's
Gastropoda	**0.037**	**0.54**	ANOVA	**0.017**	Scott's

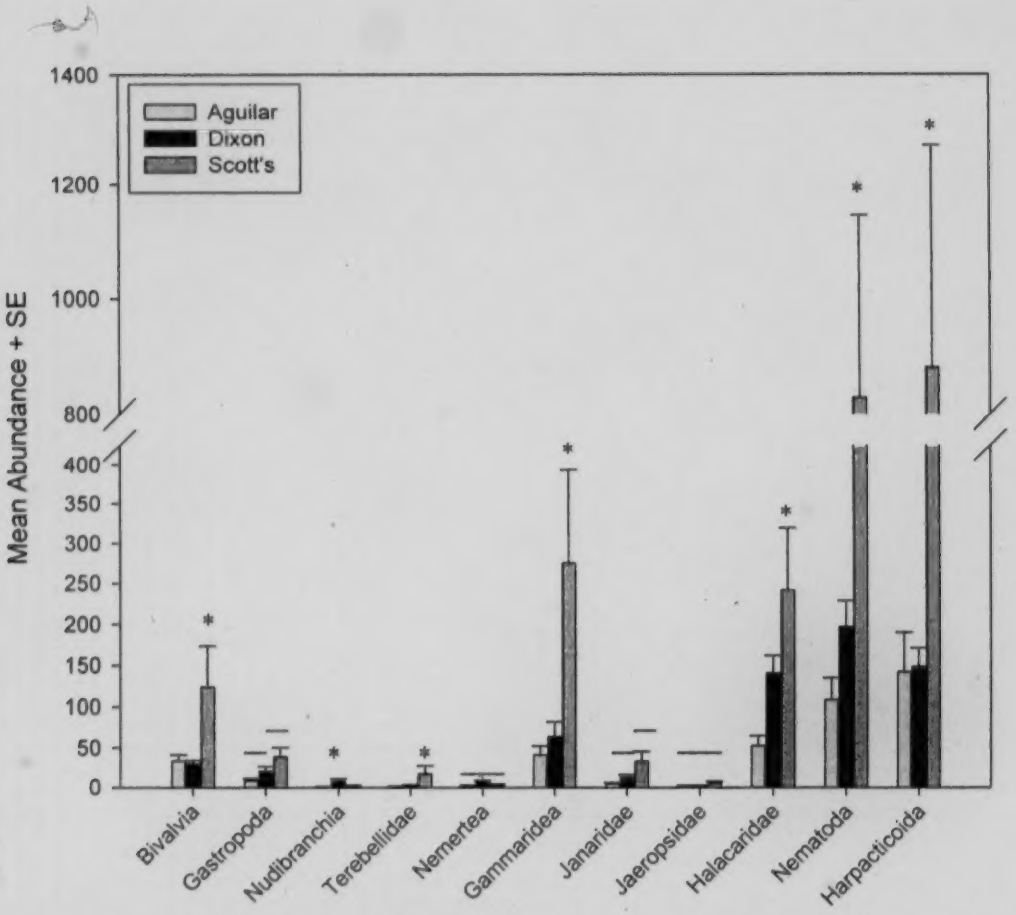

Figure 2-5. Mean abundance of significant indicator taxa of the three sites Aguilar Point (n=15), Dixon Island (n=14), and Scott's Bay (n=15). Asterisk indicates significance at level of $p<0.05$ for ANOVAs. Lines indicate similarity. Significant values for Bivalvia, Gastropoda, Nudibranchia, Nemertea, Janiridae, Jaeropsidae, and Halacaridae, Harpacticoida and Nematoda were calculated with log-10 (x+1) transformed data but presented as raw data for comparison.

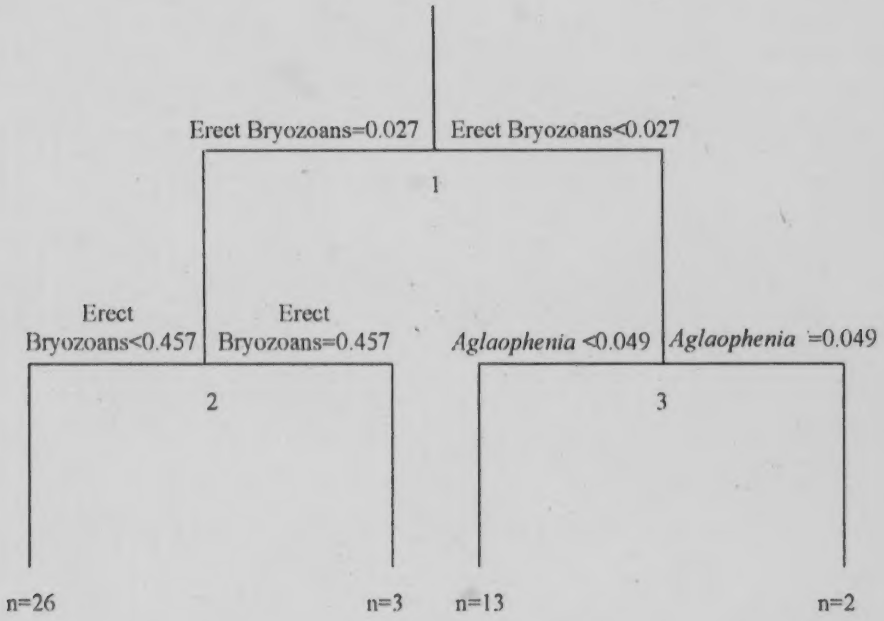

Figure 2-6 Multivariate Regression Tree of all samples (n=44). Values are the weight that corresponded with the split in the community. Numbers indicate higher node numbers. Error = 0.55, CV error =0.953, SE=0.257.

Table 2-3. Results of higher node 1 ITA (dry weight of erect bryozoans). Bold p-values indicate statistical significance at level of $p \leq 0.05$. Dagger (†) indicates t-tests, asterisk (*) indicates Mann-Whitney U tests. Gastropoda and Gammaridea were log-10 (x+1) transformed to meet assumptions of normality

	Indicator Taxon Analysis		**T-/Mann-Whitney U Tests**		
Taxon	IV	p-value	t/z value	p-value	**Max Class**
Gastropoda	0.80	**0.001**	t=-4.295†	**<0.001**	≥0.027
Gammaridea	0.87	**0.001**	t=-3.479†	**<0.001**	≥0.027
Nereidae	0.69	**0.002**	t=4.004†	**<0.001**	≤0.027
Polynoidae	0.50	**0.024**	z=-2.726*	**0.006**	≥0.027
Jaeropsidae	0.46	**0.029**	z=-2.501*	**0.012**	≥0.027

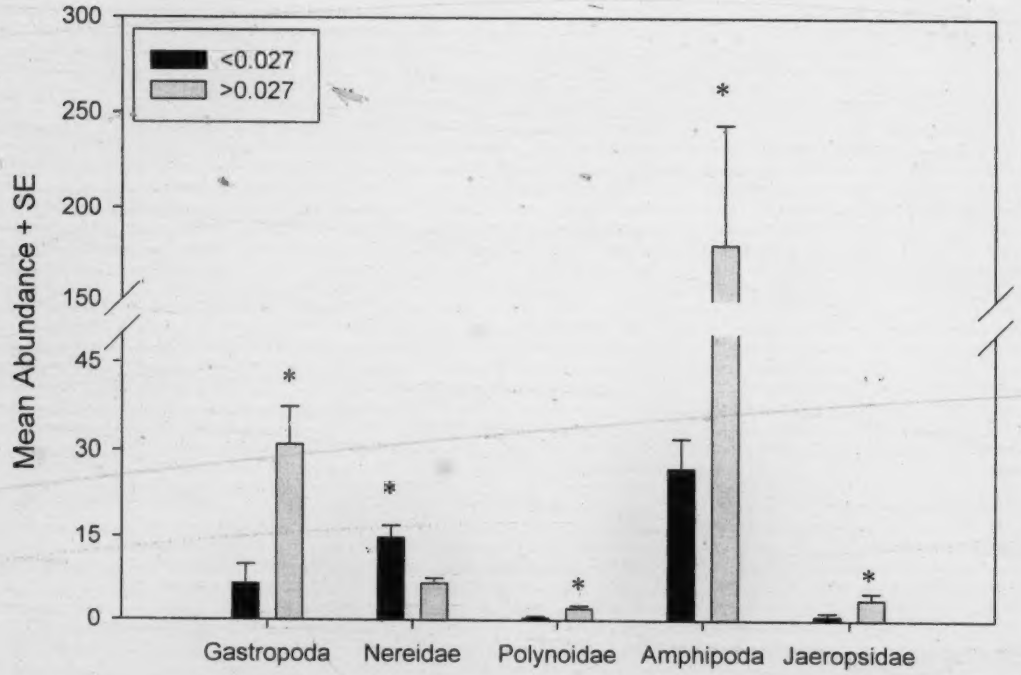

Figure 2-7. MRT node 1 comparisons between samples with ≥ 0.027 g (n=29) erect bryozoans or ≤ 0.027 g (n=15) erect bryozoans for significant taxon indicators. Asterisk indicates significance at the level of p≤0.05 for t-tests.

Table 2-4. Results for ITA for higher node 2 split by dry weight of erect bryozoans. Bold p-values indicate statistical significance at the level of p≤0.05. No additional analyses were permissible because of low sample size for class >0.457 (n=3) compared to class <0.457 (n=26).

Indicator Taxon Analysis			
Taxon	IV	p-value	Max Class
Paratanaidae	0.89	**<0.001**	>0.457
Terebellidae	0.89	**<0.001**	>0.457
Gammaridea	0.87	**0.038**	>0.457
Harpacticoida	0.87	**0.004**	>0.457
Polynoidae	0.85	**<0.001**	>0.457
Jaeropsidae	0.85	**0.013**	>0.457
Nematoda	0.85	**0.002**	>0.457
Gastropoda	0.83	**0.029**	>0.457
Halacaridae	0.79	**0.004**	>0.457
Bivalvia	0.75	**<0.001**	>0.457
Syllidae	0.73	**<0.001**	>0.457
Entoprocta	0.68	**<0.001**	>0.457
Brachyura	0.61	**0.012**	>0.457

Table 2-5. Results from ITA for higher node 3 split by dry weight of *Agalophenia* spp. Bold p-values indicate statistical significance at a level of $p \leq 0.05$. No additional analyses were permissible because of low sample size for class>0.049 (n=2) compared to class <0.049 (n=13).

Indicator Taxon Analysis			
Taxon	IV	p-value	**Max Class**
Harpacticoida	0.98	**<0.001**	>0.049
Munnidae	0.97	**<0.001**	>0.049
Janaridae	0.97	**<0.001**	>0.049
Bivalvia	0.97	**0.019**	>0.049
Nematoda	0.96	**<0.001**	>0.049
Ostracoda	0.93	**<0.001**	>0.049
Halacaridae	0.91	**0.014**	>0.049
Caprellidea	0.91	**0.011**	>0.049
Syllidae	0.91	**<0.001**	>0.049
Gastropoda	0.90	**0.011**	>0.049
Nudibranchia	0.87	**<0.001**	>0.049
Sabellidae	0.49	**<0.001**	>0.049

CHAPTER 3: EFFECT OF HEIGHT AND SAMPLING TIME ON INVERTEBRATE ASSEMBLAGES IN INTERTIDAL CORALLINE ALGAE

INTRODUCTION

One of the most striking patterns in marine ecosystems is the zonation of organisms in intertidal regions. Intertidal zonation is a widely studied phenomenon and is expressed across a variety of substrata (rocky, muddy, sandy, etc.). Perhaps the best-studied intertidal habitat is the rocky shore (Menge and Branch 2001). Though few generalizations can be made, it is widely accepted that physiological tolerances to heat and desiccation stress ultimately define the upper boundary of a species' distribution across the intertidal zone, and that biotic factors such as competition and predation set the lower boundary (Connell 1972, Raffaelli and Hawkins 1996).

As with any ecological generalization, exceptions to the rule exist, and other abiotic and biotic factors may influence the degree of zonation (Lewis 1964). These other "horizontal" forces (e.g., wave exposure, salinity, and nutrient concentration) tend to act in a perpendicular fashion to the "vertical" stress of exposure time (Harley 2003). Horizontal factors are thought to modify vertical distribution patterns, by either amplifying or tempering the effects of exposure (Harley 2003). For example, organisms on a more exposed shore may be able to survive at higher tidal heights if wave splash increases the physical range that can be occupied compared to that on a more sheltered shore with less splash. The magnitude of these changes can also be dependent on the slope of the site. These interacting factors have been well documented throughout the literature (Lewis 1964, Menge and Branch 2001, Harley 2003).

The presence of large-bodied sessile organisms in the rocky intertidal can modify both abiotic and biotic impacts on other species, and hence potentially affect zonation patterns (Nixon et al. 1971, Bertness et al. 1999, Bruno and Bertness 2001, Harley 2006). Organisms that act as habitat or substrate for other species are sometimes called 'foundation species' (sensu (Dayton 1972). Intertidal algae often act as foundation species modifying the physical habitat and acting as substrate for a variety of sessile and motile invertebrates (Menge 1978, Bertness et al. 1999, Bracken et al. 2007). Turf-forming geniculate coralline algae (Rhodophyta: Rhodophyceae) is found world-wide in the low- to mid-tidal range in rocky intertidal habitats (Padilla 1984, Dye 1993, Akioka et al. 1999, Kelaher et al. 2001). The branches of the algae mat together and alter water flow when submerged and desiccation rates when exposed (Dommasnes 1968, Padilla 1984). This results in provision of habitat for a diverse assemblage of invertebrates and some vertebrate larvae, with some studies have shown densities up to 1.6×10^6 animals m^{-2} (Huff and Jarett 2007).

A few studies have found that invertebrate assemblages inhabiting intertidal coralline algae vary according to tidal height (Kelaher et al. 2001, Kelaher et al. 2003, Kelaher et al. 2004). Polychaetes, amphipods, and gastropods showed a consistent increase in species richness between the high and low tidal heights in Australia (Kelaher et al. 2001, Kelaher 2003). Kelaher et al (2004) found intercontinental differences in effects of tidal height on gastropod assemblages in coralline algae. There were strong height differences in Australia, weak non-significant differences in Ireland, and no clear pattern in Chile (Kelaher et al. 2004). Though these studies have found a difference between assemblages at different shore heights there are still gaps in our knowledge. For

example, none of the presented studies have included sessile organisms (e.g., bryozoans, hydroids, sessile polychaetes) in their analyses due to quantification difficulties.

Southward (1958) pointed out that few studies had examined how organisms in the intertidal were distributed during the period when the shore was covered with water. Southward's observation of almost 50 years ago still holds true. In a search of the natural sciences section of Ecology Abstracts, using the key words "intertidal", "emersion" or "immersion", "invertebrate*", and "distribution", for papers before 1960 to current day, only two papers were found that had examined species distribution when underwater (Davenport et al. 1999, Hooper and Davenport 2006). Intertidal ecologists have formed many of their assumptions about how species that live in the intertidal zone behave and are distributed from observations at low tide, but often overlook what happens when the shore is completely submerged. Depending on their vertical position on the shore, invertebrates may spend the majority of their time underwater which could greatly impact how they are spatially distributed.

Although it is thought that motile fauna migrate with the falling tide, to my knowledge only two studies (Davenport et al. 1999, Hooper and Davenport 2006) have examined invertebrate assemblages in similar areas at both low and high tides. The first study, conducted in Australia, found a significant decrease in invertebrate abundance associated with three species of intertidal algae, but the degree of decrease was dependent on the fractal dimension (complexity) of the algae (Davenport et al. 1999). Invertebrates associated with *Corallina* spp., the most complex of the three species, showed the least change (Davenport et al. 1999). Hooper and Davenport (2006), in contrast, found no

difference between invertebrate assemblages at low and high tide in three other species of algae in Scotland.

Along with abundant motile epifauna, sessile and encrusting invertebrates and algae are also found on coralline algae (Hicks 1971). Attached bryozoans, sponges, and hydroids theoretically further modify the algal-mat habitat by increasing morphological complexity (Hall and Bell 1988); however, no studies of invertebrate assemblages in coralline algae have characterized the sessile epibiotic fauna and attempted to assess their impact on motile fauna.

Given these previous studies on coralline algae as habitat, my research study had three objectives. Two of them involved examining the influence of submersion on invertebrate assemblage structure, the first with regard to position relative to tidal height (height up the shore, which is equivalent to duration of exposure during low tide), and the second was whether the coralline algae at these different heights was actually submerged or exposed at the time of sampling. I predicted that organisms would be more abundant in samples taken from lower on the shore, and also in those taken when submerged. My third objective was to examine whether the presence of sessile epifauna such as bryozoans and sponges on the algae was correlated with differences in assemblage structure of the motile invertebrates. I expected that organisms would be more abundant in samples where sessile epifauna were present because of the increased structural complexity in the samples.

METHODS

Study Location

This study was undertaken at the Bamfield Marine Sciences Centre in Barkley Sound, British Columbia, Canada (latitude 48°50.08' N, longitude 125°08.8'W). Three sites were sampled in this observational study: Aguilar Point, Scott's Bay, and Brady's Beach (see Fig. 2-1). The site names correspond to the nearest recognized landmarks. The three sites are within one kilometre of one another. All shores are gently sloping (~30°-40°) rocky intertidal habitat that face northwest. The geniculate coralline algal beds are composed predominantly of *Corallina vancouveriensis* Yendo but also include *Bossiella* spp. (see Appendix 2, 3, and 4). Beds of mussels (*Mytilus trossulus* Gould and *M. californianus* Conrad) and the kelp *Egregia menziesii* (Turner) demarcate the upper and lower boundaries of the coralline turfs respectively.

Transect preparation

At each site two transects parallel to the waterline were delineated by drilling permanent endpoint bolts into the rock face. The two transects demarked "high" and "low" transects with respect to intertidal height. The "high" transect was placed just below the mussel bed and the "low" transect was placed just above the *E. menziesii* bed (Fig. 3-1). Each transect was approximately seven metres in length. The high transect at Aguilar Point was 14 vertical centimeters above the low transect, 34 cm at Brady's Beach and 30 cm at Scott's Bay

Just prior to sampling via SCUBA diving, white strings were connected between the transect bolts to make sampling easier and more precise. Neither of the previous studies (Davenport et al. 1999, Hooper and Davenport 2006) examining the effect of tidal

flooding on intertidal assemblage structure left markers to maintain a constant position on the shore for the different sampling periods.

Field Sampling

Algal sampling took place from 10 June to 12 June 2006. At each site, ten 'exposed' algal tufts (those taken when the tide was out and the tufts were exposed to air) were haphazardly collected from each of the two transects by removing the algae from the rock and placing the samples into individual whirl packs (n=20 samples per site for a total of 60 'exposed' samples). The exposed samples for Aguilar and Scott's Bay sites were taken on 10 June 2006 and the Brady's Beach site was sampled on 11 June 2006. On 12 June 2006, two SCUBA divers (I and a volunteer) went to the three sites and collected ten 'submerged' algal tufts from each of the two transects per site, again by removing the tufts by hand and placing them in individually labeled whirl packs (n=20 per site for a total of 60 'submerged' samples). All samples were returned immediately to the laboratory for processing.

Laboratory Analysis

All samples were brought back to the lab and were sieved through a 53 μm mesh and the material retained in the mesh was fixed in a 4% Formalin solution. Samples were later transferred into 80% ETOH and stained with a Rose Bengal solution which binds to the proteins in the invertebrates making them easily visible against a pale background.

Of the twenty samples collected from each transect, ten (five 'exposed' and five 'submerged') were randomly selected and examined under stereromicroscopes at 25X (Leica MZ 16 and Leica Wild Heerburgg) for all identifiable invertebrates (the head had to have been present to be counted). This was done by placing the sample in a gridded

Petri dish and systematically working through the dish. All clumps of algae were teased apart to remove all animals from the fronds. Invertebrates found were identified to the following taxonomic levels. Taxa identified to phylum were nemerteans, nematodes, and ectoprocts (hereafter called bryozoans). Organisms identified to class were poriferans, cnidarians, and molluscs. Due to the varying degrees of difficulty of identification, annelids were identified to either class or family, and arthropods were identified to class, order, suborder or family (see Appendix 2, 3, and 4 for details and level of taxonomic resolution). Identifications were done using the Leica MZ 16 at 25 - 115X with the aid of three taxonomic manuals: (Smith and Carlton 1975, Hayward and Ryland 1985, Kozloff 1999). Solitary organisms were completely enumerated and are presented as the number of individuals per sample. A very large number of nematodes (>500) were present in six of the sixty samples sorted, so I subsampled the nematodes from these samples (see nematode subsampling section below). Sedentary colonial animals attached to algae were grouped into two categories, those likely to act as habitat for other animals (e.g. sponges), and those unlikely to act as habitat themselves (e.g. very small hydroid colonies). These were recorded as present or absent.

The bryozoans *Filicrisia franciscana* (Robertson, 1910), Flustrellidra spp, and various species of encrusting bryozoans were removed from the coralline algae, placed onto Whatman filter paper (42, ashless circles, 90 mm diameter) dried in a 60°C oven for 24 hours and weighed (to 0.001 of a g) to account for other sources of biogenic habitat in the samples. Sponges and hydroids could not be weighed as habitat forming species because they were too difficult to extricate from other colonial animals and epiphytic algae. They were instead accounted for by simple presence/absence data. Along with the

metazoan animals that were counted and identified, other organisms such as foraminiferans, and some epiphytic algae were found in the samples but they were not quantified or identified.

The coralline algae from all the sorted samples was cleaned of sessile invertebrates, epiphytes and fouling agents, dried in a 60° drying oven for 24 hours and weighed (to 0.001 of a g).

Nematode Subsampling

Six samples were subsampled for nematodes (see Appendix 2,3, and 4). Subsampling occurred once all coralline algae and other sessile animals and epiphytes had been removed. 80% ethanol was added to samples to make the total volume 60 mL. The sample was then stirred to suspend the animals, a 6 mL subsample was removed using a pipette, and all nematodes in that subsample were counted. The subsample was returned to the initial sample which was then topped back up to 60 mL if necessary. This process was completed five times for each sample and an average number of nematodes per sample was calculated. This average was then multiplied by ten and used as the number of nematodes per sample.

Data Analysis

All data was organized using Microsoft Excel 2004 for Mac (version 11.3.5). Several statistical packages were used for analysis of data. Univariate data was analyzed using SPSS 13 for Mac OS X (version 13.0.0). Multivariate data was analyzed using PATN (version 3.03) and R (version 2.5.1 GUI 1.20).

Regressions of the total number of individuals/algal weight per sample and total number of taxa/algal weight per sample, done using SPSS, demonstrated significant

positive relationships (see results below for details). Therefore, all further analyses were performed on data standardized per unit weight of algae. Each taxon was standardized to one gram of algae by dividing the count by the dry weight (g) of coralline algae sampled (see Appendix 2,3, and 4 for initial and standardized values).

Data were grouped into three *a priori* categories for multivariate analysis: site (Aguilar, Brady, Scotts), exposure (exposed, submerged), and transect height (high, low). Raw data were used for all motile invertebrate taxa except for nematodes, which were typically an order of magnitude more abundant than any other taxon. Nematode data were therefore log-10 transformed prior to analysis to prevent them swamping the data, allowing other organisms more influence in the ordination. Data were ordinated in PATN with semi-strong hybrid multidimensional scaling (SSH-MDS) using Bray-Curtis distance measures and 1000 random starts. For each of the three *a priori* categories, Bray-Curtis distances were analyzed with a multivariate analysis of similarity (ANOSIM) in PATN with 1000 permutations to determine if any categorizing variable was associated with significant differences in invertebrate assemblage structure. Monte-Carlo Attributes in Ordination (MCAO) and Principle Component Correlation (PCC) were also run to determine important vectors for each of the three ordinations. Vectors were selected based on two factors: MCAO results of less than one percent and an r^2 of greater than 0.5 in the PCC.

To determine which taxa explained the differences between the categorizing variables (site, exposure, and height), indicator species analyses (ISA) (Dufrene and Legendre 1997) were run using the duleg function in the labdsv library with 1000 iterations in R. Since I was using the ISA on higher taxonomic groups, it is more

properly called indicator taxon analysis (ITA). Indicator taxon analyses in R (R Development Core Team 2005) provide a p-value as well as an indicator value (IV), which ranges from 0 (no indication) to 1 (perfect indication); values greater than 0.6 are generally considered good indicators (Jacobs et al. 2007). All taxa that received a significant p-value from the ITA ($p<0.05$) were then later examined with appropriate univariate statistics (t-tests, ANOVA, Kruskall-Wallis, Mann Whitney U).

A two-way multivariate analysis of variance (2-way MANOVA) using exposure and tidal height as response variables was run to determine if there was any interactions between these two factors. Post hoc protected ANOVAs were also run to locate significant univariate effects.

A multivariate regression tree (MRT) was used to identify environmental factors that split the data in a way that minimized dissimilarity within clusters (De'Ath 2002). Factors included in the MRT were site, transect height (high/low), exposure (exposed/submerged), weight of *Filicrisia franciscana*, weight of *Flustrellidra* sp., weight of encrusting bryozoans, and total 'substrate' weight. The MRT was run using the R package (R Development Core Team 2005) using the mvpart library (Therneau and Atkinson 2005) with a Bray-Curtis distance matrix. The MRT analysis was run 20 times and only one tree was produced. MRT trees consist of terminal nodes and higher nodes. Residual error, standard error, and cross-validated errors accompany the tree. The cross-validated error (CV) is the predictability power of the tree and ranges from 0 (perfect prediction) to 1 (no prediction) but can range above 1 in some circumstances. The "best" tree is generally considered the tree with the lowest CV error (De'Ath 2002). For each higher node, an ITA was conducted to determine the organisms driving the split.

Appropriate post-hoc univariate analyses were then completed to determine where the differences lay.

All figures were made with SIGMAPLOT 13.0 for PC.

RESULTS

Overall, a total of 15 506 individual animals were identified from eight invertebrate phyla, five of which are predominantly motile (Nematoda, Arthropoda, Annelida, Mollusca, and Nemertea) and three sessile (Ectoprocta (bryozoans), Cnidaria, and Porifera). Nematodes were the most abundant phylum representing 67% of the individuals found, and arthropods were the second most abundant at 19% of all individuals.

Relationship between taxon richness, total number of individuals and algal weight

There was a significant positive relationship between the taxon richness and the dry weight (g) of algae collected for the samples ($p<0.001$, $r^2=0.24$), and between total number of individuals and weight of algae ($p<0.001$, $r^2=0.27$) (Fig. 3-2). These relationships held when the data were divided into sites, exposures, and transect heights except for Aguilar taxon richness ($p=0.584$, $r^2=0.017$) and submerged taxon richness when an extreme outlier was removed ($p=0.587$, $r^2=0.011$). Prior to the outlier being removed, $p=0.011$, $r^2=0.21$.

Site

The analysis of the three sites was done to determine if sites could be used as replicates or if they should be analyzed separately. When an analysis of similarity (ANOSIM) was run on the community matrix of the SSH-MDS, there was no site that was statistically significantly different from another: Aguilar vs Brady's $p=0.08$, Aguilar

vs Scott's p=0.41, Brady's vs Scott's p=0.06 (Fig. 3-3). As there was no significant difference between the sites, they have been grouped together for all further analyses. Significant vectors included halacarid mites, harpacticoid copepods, and bivalves (these vectors are the same for the effect of height and the effect of exposure).

Indicator taxon analysis showed that nematode abundance differed among the three sites ($p<0.001$); however, the indicator value (IV) is quite low (IV=0.38). Nematodes were significantly more abundant in samples from Brady's Beach than in those from Aguilar Point and Scott's Bay (ANOVA p=0.003, df=2, F=6.317) (Fig. 3-4).

Effect of Height

ANOSIM show no significant overall difference in invertebrate assemblages between high and low transects (ANOSIM p=0.059) (Fig. 3-5); however, post-hoc ITA and subsequent t-tests revealed that sphaeromatid isopods (ITA: p=0.014, IV=0.2267) and nematodes (ITA: p=0.027, IV=0.6922) were both significantly more abundant in high transects (t-test: p=0.013, df=58, t-value=2.573; Mann-Whitney U test: p=0.015, df=58, z=-2.427, respectively) (Table 3-2). Caprellid amphipods (p=0.017, IV=0.2918), ostracods (p=0.017, IV=0.4032), and larvae of gastropods (p=0.49, IV=0.1881) were significantly more abundant in low transects (Mann-Whitney U test: p=0.029, df=58, z=-2.19; Mann-Whitney U test:p=0.021, df=58, z=-2.299; Mann-Whitney U test:p=0.041, df=58, z=-2.042, respectively) (Fig. 3-6). There was significantly greater abundance of invertebrates in high transect samples (log 10 transformed t-test: p=0.045, df=58, t=2.05) (Fig. 3-7), but greater taxon richness in the low transects (log 10 transformed t-test: $p<0.001$, df=58, t=-3.532) (Fig. 3-7). When nematodes were removed from the

abundance calculations, there was no significant difference between the two heights (log 10 transformed t-test: p=0.176, df=58, t=1.371).

Effect of Exposure

Results of the ANOSIM revealed a significant difference in assemblage structure between samples taken when transects were exposed vs submerged (p=0.001) (Fig. 3-8). Post-hoc univariate comparisons between the two treatments showed no difference in the total number of individuals collected at either tidal régime when data was log-10 transformed (except nematodes which were already transformed and met normality) to meet assumptions of normality and equal variance (p=0.727, df=58, t=0.35) (Fig. 3-9). There was, however, a difference in the mean taxon richness per sample between exposed and submerged samples, with submerged samples having greater taxon richness (p=0.001, t=-3.424, df=45.869) (Fig. 3-9). The ITA showed that 4 taxa were significantly different between the two exposures (Table 3-3). Nereid polychaetes (ITA: p<0.001 IV=0.676) were significantly more abundant in exposed than submerged samples (t-test: p<0.001, t=4.497, df=58) (Fig. 3-10). Calanoid copepods (ITA: p<0.001, IV=0.100) were only found in submerged samples; however, this was not significantly different between treatments (Mann-Whitney U test: p=0.078). Nemerteans (ITA: p=0.033, IV=0.202), though more abundant in exposed samples, were also not significantly different from the submerged samples (Mann-Whitney U test: p=0.057). Nematodes (ITA: p=0.035, IV=0.2287) were significantly more abundant in the exposed samples (t-test: p=0.043, df=58, t-value=2.067) (Fig. 3-10).

Two-way MANOVA revealed no significant interaction between the two response variables of transect height and exposure, but did show differences between

exposed and submerged samples as well as between high and low samples (see Appendix 5 for results). Post hoc ANOVAs for exposed and submerged samples found nereid polychaetes, nemerteans, and nematodes were significantly different ($p<0.05$). Ostracods, gastropod larvae, sphaeromatid isopods, and nematodes were significantly different between the high and low samples as identified by the post hoc ANOVAs ($p<0.05$).

Environmental Factors Correlated With Assemblage Structure (MRT)

The multivariate regression tree was run with the following potential explanatory factors: dry weight of *Flustrellidra* sp., dry weight of encrusting byrozoan, dry weight of *Filicrisia franciscana*, transect height, exposure, site, presence or absence of sponges, and the total weight of all substrates (coralline algae plus bryozoan weights). The MRT had one higher node and two terminal nodes relating to the presence or absence of the erect bryozoan *Filicrisia franciscana*. However, this explained little of the variation of the data (8%) and had a high cross-validated error (CV error=1.07) and therefore low predictability power (De'Ath 2002). There were both statistically significantly more individual invertebrates per sample (t-test log-10 transformed: t=-3.155, df=58, p=0.003) and greater taxon richness per sample (t-test log-10 transformed: t=-4.145, df=58, $p<0.001$) in samples with *F. franciscana* than in those without (Fig. 3-11). Subsequent ITA showed six taxa (halacarid mites, bivalves, gastropod larvae, caprellids, ostracods, and syllid polychaetes) responded to the presence of *F. franciscana* and were all significantly more abundant in samples where the erect bryozoan was present (Table 3-4, Fig. 3-12).

DISCUSSION

Geniculate coralline algae acts as home for a wide diversity of associated invertebrates in Barkley Sound. Overall, invertebrate assemblages inhabiting coralline algae do not differ significantly between sites examined (Fig. 3-3), or between low and high transects (Fig. 3-5), but do differ significantly between samples collected at low (exposed) and high (submerged) tide (Fig. 3-8). There were statistically significant positive relationships between the dry weight of coralline algae in a sample and both the taxon richness and the total individuals per sample This provides support for two ecological theories or a combination of the two: first, the well-known species-area relationship, where greater amounts of habitat can support great number of species (Connor and McCoy 1979, Hoyle 2004); second, the theory that increase morphological complexity, associated with higher algal biomass, increases the number of habitable niches (MacArthur and MacArthur 1961, Hicks 1980). Which theory is best supported by the present study is unclear, given that an increase in amount of algae will likely increase both complexity and surface area. Though many studies have found that increases in habitat complexity increase species diversity (Hall and Bell 1988, Gee and Warwick 1994, Hull 1997), few have attempted to disentangle complexity from habitable area (Beck 2000). Beck (2000) found that both surface area and structural components increase species diversity. Further studies would be required to separate these two theories in this relationship.

Site

There was no statistical difference between the three sites when compared using ANOSIM thereby allowing sites to be used as replicates for this study. Although the log

abundance of nematodes was a significant indicator of different sites ($p<0.001$), the indicator value was quite low (IV=0.38) suggesting that the nematodes cannot be used reliably as an indicator of the three sites. The ANOVA results reveal that the difference in nematode abundance lies between the Aguilar and Scott's sites compared to Brady's Beach site. This is likely due to two samples in the Brady's Beach site with extremely high numbers of nematodes ($n>1000$) (see Appendix 3). The similarity of the three sites lends support to the theory that invertebrate assemblages may be similar over larger spatial scales but may be patchy within a single site (Menconi et al. 1999, Benedetti-Cecchi 2001, Kelaher et al. 2004).

Vertical Height of Transects

ANOSIM showed no difference in invertebrate assemblage structure between the high transects and the low transects. This lack of differentiation was surprising, as many other studies have shown that height in the intertidal correlates to increases in abiotic stress (primarily exposure to desiccation) and is important in determining how species are distributed within this zone (Lewis 1964, Raffaelli and Hawkins 1996, Araujo et al. 2005). My observations are in direct contrast to work done in Australia (Kelaher et al. 2001, Kelaher et al. 2003, Kelaher et al. 2004), which showed a clear differentiation between assemblages of invertebrates inhabiting coralline algae at different tidal heights. However, the patterns were not consistent over continental geographical ranges (Kelaher et al. 2004). It is possible that the hotter, sunnier semitropical Australian climate may result in greater impacts over smaller vertical intertidal ranges compared to the cooler rainier British Columbian weather.

Although taken as a multivariate whole, assemblage structure did not differ between high and low transects, there were univariate differences between samples taken from different shore heights. Taxon richness was greater in low-shore samples but abundance was greater in high-shore samples. ITA identified nematodes and sphaeromatid isopods as significantly more abundant in high transects (Fig. 3-6); and caprellid amphipods, ostracods, and gastropod larvae as significantly more abundant in low transects (Fig. 3-6); however, only nematodes should be used as indicators as the other species had quite low indicator values ($IV \leq 0.40$).

Greater taxon richness in low transects could be expected because it represents less physiologically stressful habitat, allowing for a wider diversity of invertebrates to exploit the niche. Mean total abundance per sample is not as straightforward. There is no clear explanation for why invertebrates would be more abundant in the high-shore transects, unless there are a few, numerically abundant taxa that prefer high-shore habitats, or that are associated with some other biotic factor found in high-shore transects. In fact, when nematodes are removed from the total abundance values, there is no difference in mean total abundance between transect heights, suggesting that the high relative abundance of nematodes is swamping the results.

The greater abundance of gastropod eggs in the lower intertidal suggests that gastropods have chosen the less abiotically stressful habitat as oviposition sites, but the adults are not found more frequently in this particular habitat. This could support the idea of niche partitioning; it is possible that juvenile gastropods inhabit the lower intertidal and the adults are able to move more freely between habitats.

Sphaeromatid isopods are known to occupy a wide range of habitats and are tolerant of desiccation (Hass and Knott 1998). Their greater abundance in the more abiotically stressful environment may be indicative of this increased tolerance and their ability to leave more competitive intertidal zones in favor of increased physiological stress.

Caprellid amphipod species which generally have wide species ranges, respond to local environmental conditions and tend to be found more abundantly in subtidal than intertidal zones (Thiel et al. 2003). This may suggest why they are more abundant in the lower intertidal where they are less exposed to harsh conditions.

Though several differences were found between low and high transects, nematodes are the only taxon statistically supported by the results of the indicator taxon analysis as having both a significant p-value and a relatively high indicator value (IV=0.6922). I believe that the strikingly higher nematode abundance in high transects is primarily due to their association with a particular filamentous epiphytic alga found on the coralline algae (personal observation). Although unfortunately, presence or absence of this alga in a sample was not consistently noted, I believe there is a correlation between its presence and increased nematode abundance. It would be interesting to examine this association in future studies. Nematodes in general are the most abundant group of marine meiofauna (Chinnadurai and Fernando 2007). Epiphytic nematodes are often correlated with increased sediment and detrital loading within host algae and not necessarily with the species of the host itself (Heip et al. 1985). Of course, other factors not measured could be exercising greater influence on nematode distribution and abundance rather than position in the intertidal.

One reason why no difference was found in invertebrate assemblages over the two tidal heights may be that the complexity of the coralline algae mitigated the effects of the normally prevailing abiotic factors. It is possible that the coralline algae is holding enough water among its fronds to largely reduce the impact of exposure to air on the invertebrates, thereby decreasing the desiccation stress and decreasing the difference in typical zonation distribution. Dommasnes (1968) found that intertidal coralline algal turfs protected associated invertebrate communities from desiccation. Serrano and Preciado (2007) found the same but also determined that the algae provided protection from predators. Whether algae provides protection from predators may itself depend on how complex the algal turf is. Initially, mitigation of abiotic stresses by algal canopies may actually allow increased feeding efficiency of predators; however, this mitigating effect works to a threshold after which canopies that are too dense can hinder predator efficacy (Menge 1978). Removal of overstory canopy had lethal effects on understory algae because of exposure to excess desiccation, light and physical stress (Dayton 1975). It is possible that the coralline algae is holding enough water within its fronds to largely reduce the impact of exposure to air on the invertebrates, thereby decreasing the desiccation stress and decreasing the difference in typical zonation distribution.

Though the algae may have some mitigating role on abiotic factors, it is also possible that the overall difference in vertical height sampled (though it was the maximum possible given the distribution of the algal turf) was not great enough for abiotic factors such as desiccation to influence the distribution of the invertebrates. Seed (1996) found increased epifaunal diversity in mussel beds in North Wales moving from high shores to mid-shores, however, no quantitative difference in height was given.

Unfortunately, it is difficult to compare to other studies as no other studies report the actual differences between the transect heights. Another potential reason that invertebrate assemblages did not differ between tidal heights could be the taxonomic resolution of the study. Since I chose to examine most of the community, rather than focusing on one phylum, most groups were identified to class with few groups identified to finer levels. This coarse level of taxonomic resolution may have hidden some species- or genus-level patterns.

Exposure

ANOSIM showed that there was a significant difference between invertebrate assemblages sampled when exposed (at low tide) and when submerged (at high tide). There was no difference in mean total abundance of invertebrates between exposed and submerged samples (Fig. 3-9) but there was a significant difference in taxon richness (Fig. 3-9). These results are in direct contrast to (Davenport et al. 1999) who found a difference in overall abundance but no difference in taxon richness between 'exposed' and 'submerged' samples of *Corallina* sp from Australia. Four taxa (nereid polychaetes, nematodes, calanoid copepods, and nemerteans) were identified by the indicator taxon analysis as being significant in differentiating exposed and submerged samples, but based on ANOVA t-tests only nereids and nematodes were significantly different between the two sampling periods (Fig. 3-10), and both were more abundant in the exposed samples. A total of three calanoid copepods ten nemerteans were found in the 60 samples. Due to such low collection numbers, no statistical or biological conclusions can be drawn as to the preferred habitat of these organisms.

My initial concern was that the lower numbers of these animals in submerged samples may be the result of their particularly prone to being washed off during the SCUBA collection. To test this idea, I compared the numbers of a family of polychaetes morphologically and ecologically similar to Neridae, the Syllidae, on exposed and submerged samples to see if the trend toward more individuals on exposed samples was consistent. There was no significant difference between number of syllids on exposed or submerged samples (t-test p=0.278, df=58, t=-1.095); in fact, there was a slight trend towards more syllids in submerged samples. This suggests that the pattern seen in the nereid polychaetes is truly due to their higher abundance in exposed samples rather than it being an artifact of collection method.

Though it is not immediately clear as to why nereid polychaetes and nematodes are more abundant in the more physiologically challenging environment, there are some possible explanations. Nereids create mucus tubes inside coralline algae fronds that they rest in (Fauchald and Jumars 1979), it is possible that these tubes are easier to attach to coralline algae than to the rocky substrate. It is also possible that the nematodes are choosing the moist habitat to remain in while the tide is low and are also foraging when the tide is high.

Role of Environmental Factors and Habitat Forming Invertebrates

MRT results showed that the dominant 'environmental' factor (among which I included sessile epifauna that increase habitat heterogeneity) influencing the invertebrate fauna was the presence or absence of the erect bryozoan *Filicrisia franciscana*. All invertebrate taxa identified by the indicator taxon analysis were significantly more abundant in samples with *F. franciscana* (Fig. 3-11). Unfortunately, there is little

information about the biology of *F. franciscana* in the literature, and what exists is predominantly species lists from surveys (Pequegnat 1964, Parker and Tunnicliffe 1994).

There are several possible explanations for why the presence of *F. franciscana* is so strongly correlated with assemblage structure. It is possible that the bryozoans are increasing the complexity and heterogeneity of the environment and providing more habitable niches. Caprellid amphipods in particular are known to inhabit erect bryozoans (Thiel et al. 2003). It is also possible that the associated motile fauna are feeding on the bryozoans themselves (Hayward and Ryland 1985). Another potential reason for increased abundance of organisms in samples with sessile epifauna could be age related. There is a positive correlation of epiphyte mass and age on seagrasses (Hall and Bell 1988) and it is possible that the same may be true for epifauna on coralline algae. This being the case, samples with greater amounts of epifauna may be older and invertebrate assemblages may have had more time to colonize the substrate. Manipulative experimentation could elucidate which one or more of these three proposed reasons is most likely.

Other Possible Explanatory Variables

There are many more biotic and abiotic factors that could have an influential role on invertebrates inhabiting coralline algae than I measured in this study. Some previous work has demonstrated the importance of frond length of algae (Kelaher 2003) and of sediment and sand loading within the fronds in influencing how organisms are distributed within turf-forming species (Hicks 1980, Gibbons 1988, Huff and Jarett 2007). Other biotic factors to examine could include slope of the shore, maximum wave velocity, micromorphological properties of the algae, comparison to communities in tidepools, and

a host of other factors. It would also be interesting to determine if epiphytic algae help shape invertebrate assemblage structure.

CONCLUSIONS

Based on the results of this study, the presence or absence of the erect bryozoan *Filicrisia franciscana* had the greatest impact on assemblages of invertebrates inhabiting the coralline algae tufts. This proves interesting as this factor is more influential than the abiotic desiccation gradient that is normally so important in species distribution in the intertidal (Lewis 1964, Raffaelli and Hawkins 1996). Some reasons for this could be that properties of the foundation alga species could be mitigating the abiotic factors, or the vertical range of collection was not great enough to observe that vertical variation in community structure. Further studies need to be conducted to determine the extent to which the complexity of coralline algae can mitigate the harsh abiotic factors in the intertidal. As well, more ecological studies should be devoted to the roles that *F. franciscana* and other sessile colonial invertebrates play in structuring invertebrate assemblages in algal turfs.

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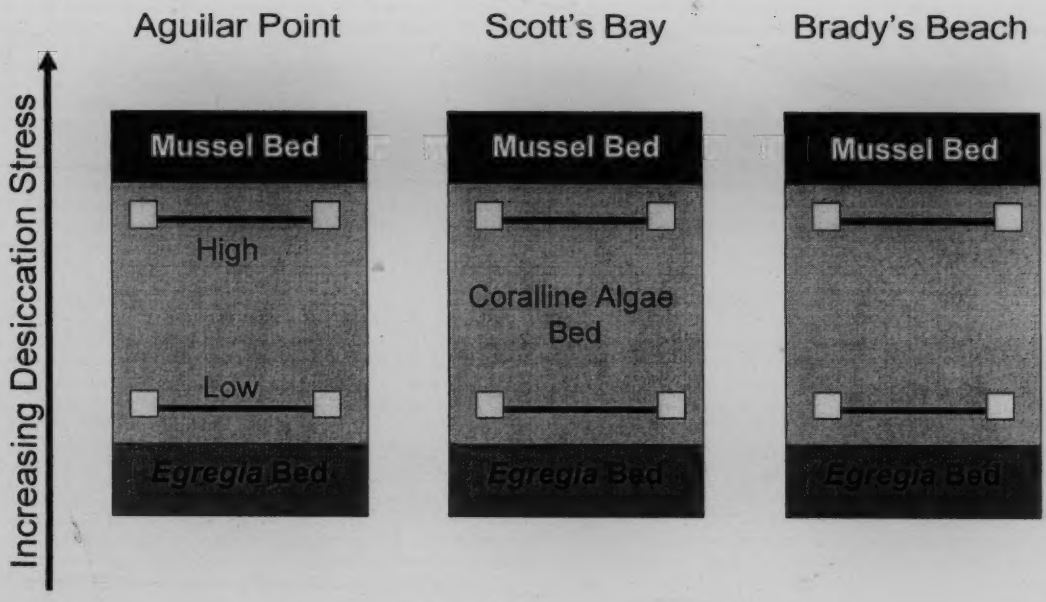


Figure 3-1: Transect design at the three sites: Aguilar Point, Scott's Bay, and Brady's Beach. Note that 10 algal tufts were sampled from each transect once at low tide from the shore (exposed samples) and once at high tide by SCUBA diving (submerged samples).

Table 3-1: Taxa and number of individuals from the 60 intertidal samples.

Phylum	Lowest Taxonomic Ranking	Total individuals	Percentage
Nematoda	Nematoda	10448	67.76%
Arthropoda	Harpacticoida	1594	10.34%
Mollusca	Bivalvia	975	6.32%
Arthropoda	Halacaridae	718	4.66%
Annelida	Nereidae	552	3.58%
Arthropoda	Naupliar larvae	477	3.09%
Annelida	Syllidae	222	1.44%
Arthropoda	Gammaridea	109	0.71%
Annelida	Oligochaeta	89	0.58%
Arthropoda	Ostracoda	48	0.31%
Mollusca	Gastropoda	48	0.31%
Mollusca	larvae of Gastropoda	42	0.27%
Arthropoda	Caprellidea	32	0.21%
Arthropoda	Chironomidae	18	0.12%
Arthropoda	Sphaeromatidae	11	0.07%
Nemertea	Nemertea	10	0.06%
Arthropoda	Janiridae	8	0.05%
Mollusca	Polyplacophora	6	0.04%
Arthropoda	Munnidae	4	0.03%
Arthropoda	Calanoida	3	0.02%
Annelida	Sabellidae	2	0.01%
Arthropoda	Idoteidae	2	0.01%

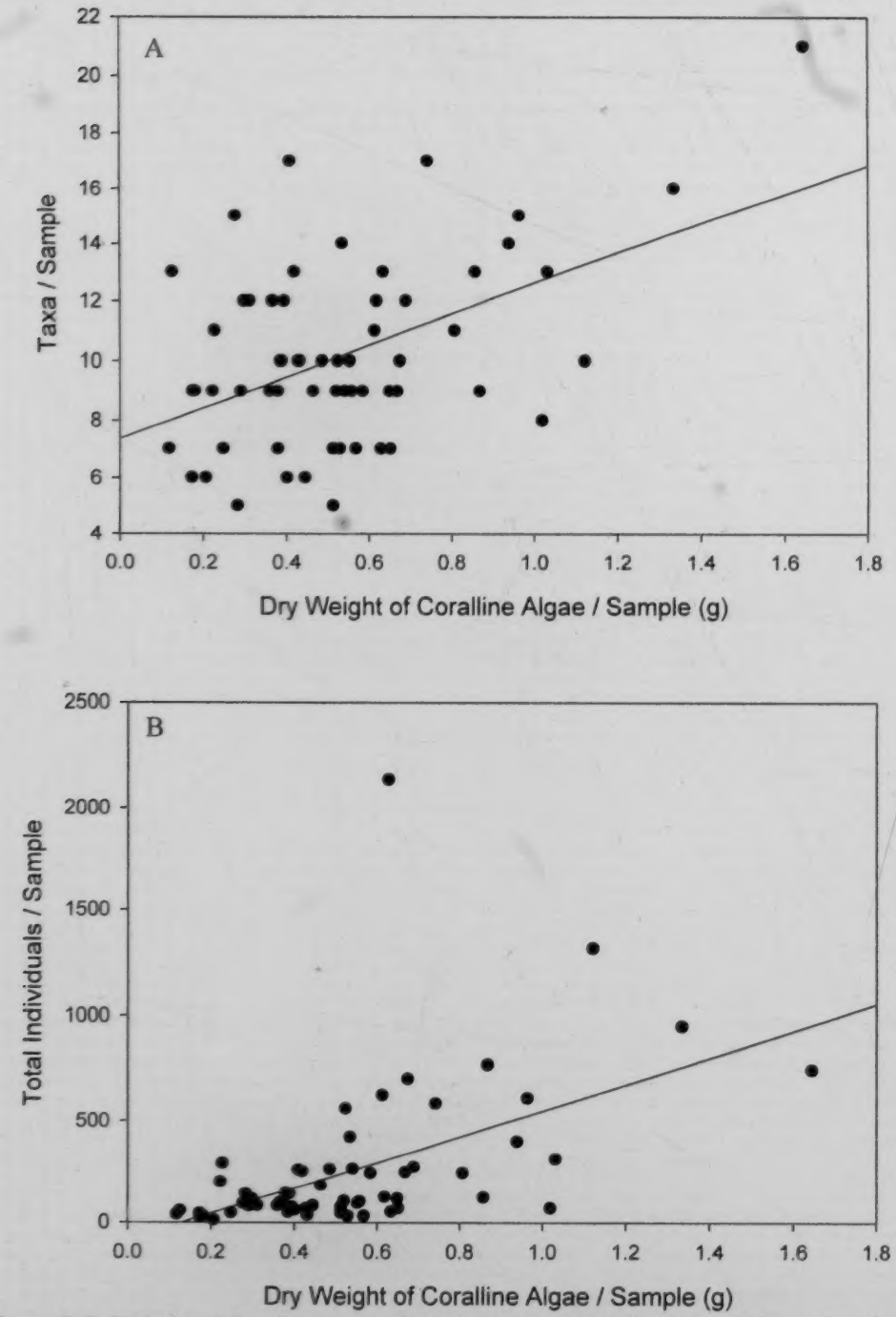


Figure 3-2: Relationship of invertebrate richness and abundance to dry weight of coralline algae per sample. A) Taxon richness (Regression $p \leq 0.001$ $R^2=0.27$). N=60. B) Total individuals per sample (Regression $p \leq 0.001$ $R^2=0.24$). N=60.

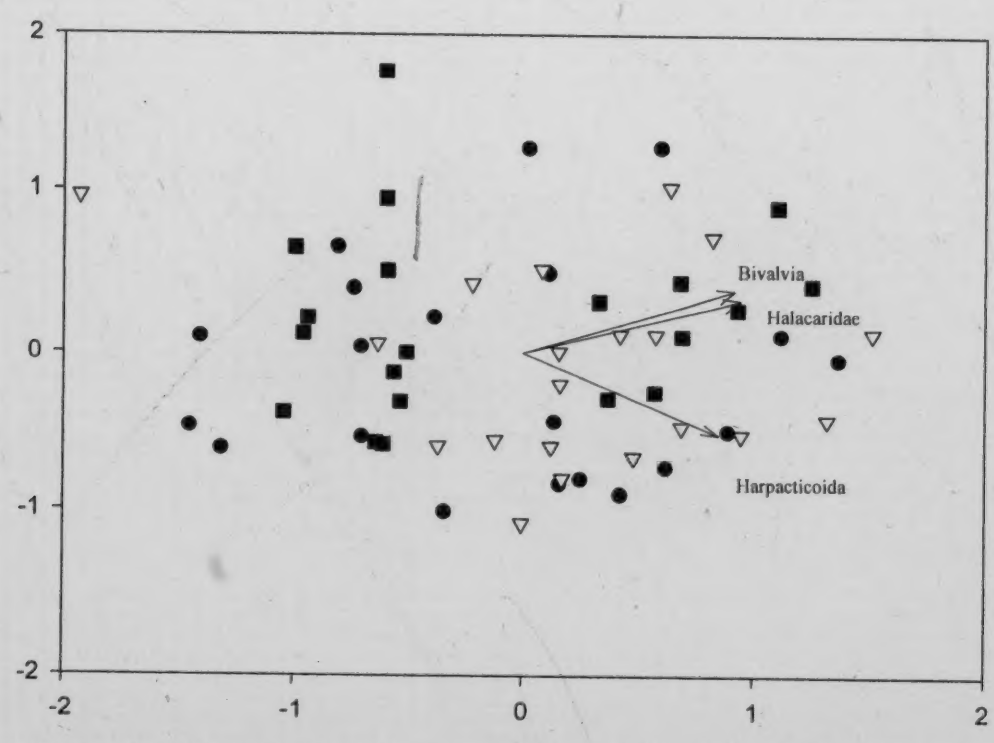


Figure 3-3: Two dimensional semi-strong hybrid multidimensional scaling (SSH-MDS) ordination comparing invertebrate assemblages at the three sites: Aguilar Point (circle) Brady's Beach (triangle) and Scott's Bay (square). Nematodes are log 10 (x+1) transformed. SSH-MDS stress = 0.22, ANOSIM A/B p=0.08, A/S p=0.41, B/S p=0.06. Vectors shown are significant at MCAO $p \leq 0.01$ and PCC r^2 of greater then 0.5. N=20 per site.

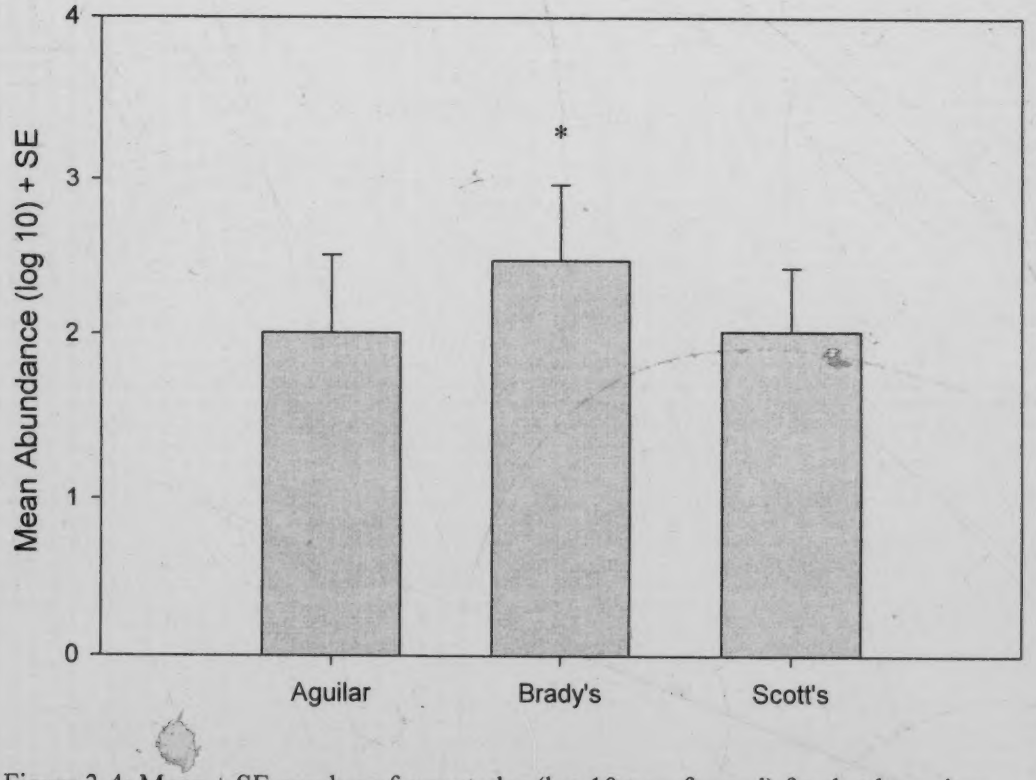


Figure 3-4: Mean + SE number of nematodes (log 10 transformed) for the three sites (Aguilar Point, Brady's Beach and Scott's Bay). Asterisk represents a significant difference (ANOVA p=0.003). N=20 algal samples per site.

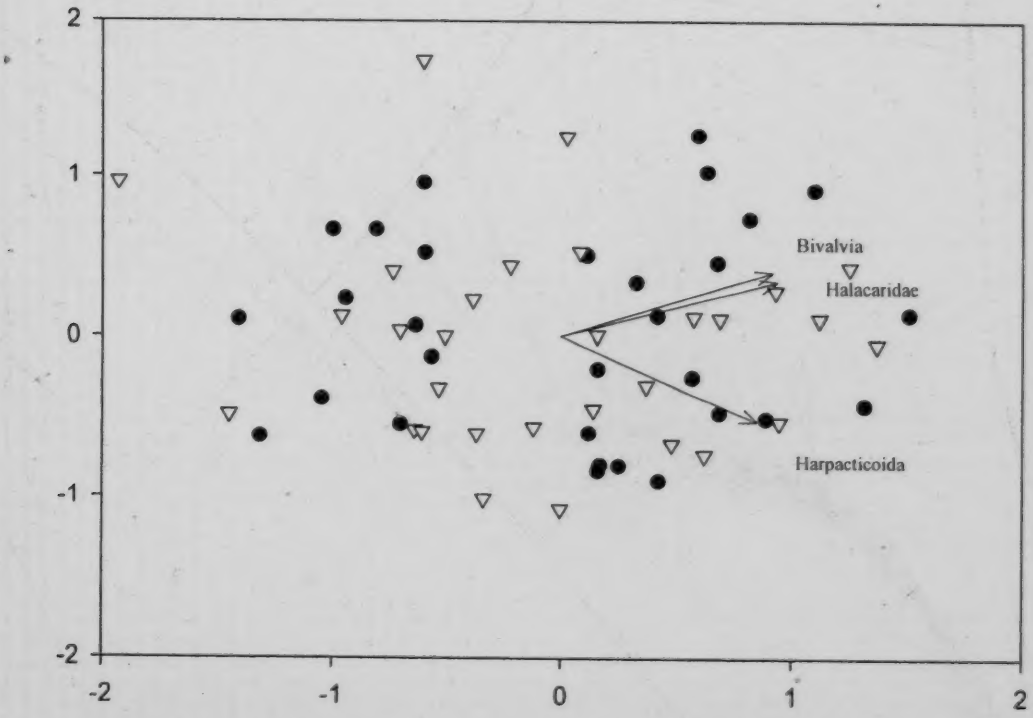


Figure 3-5: Two-dimensional semi-strong hybrid multidimensional scaling (SSH-MDS) ordination comparing invertebrate assemblages between high transects (circle) and low transects (triangle). Stress=0.22. Nematodes are log-10 (x+1) transformed. High and low transects do not differ significantly from each other (ANOSIM p=0.59). Vectors shown are significant at MCAO $p \leq 0.01$ and PCC r^2 of greater than 0.5. N=20 algal samples per site

Table 3-2: Indicator taxon analysis results and subsequent t-test or Mann-Whitney U test for comparing assemblages at high and low transects on the shore. Bold p-values indicate statistical significance at level of $p \leq 0.05$. Dagger (†) indicates t-tests, asterisk (*) indicates Mann-Whitney U tests. Mites were log 10(x+1) transformed to meet assumptions of normality.

	Indicator Taxon Analysis		**T-/Mann-Whitney U Tests**	
Taxon	Indicator value	p-value	t/z value	p-value
Nematoda	0.6922	**0.027**	t=2.573†	**0.013**
Ostracoda	0.432	**0.017**	z=-2.299*	**0.021**
Caprellidea	0.2918	**0.017**	z=-2.19*	**0.029**
Sphaermatidae	0.2267	**0.014**	z=-2.427*	**0.015**
Larvae of gastropoda	0.1885	**0.049**	z=-2.042*	**0.041**

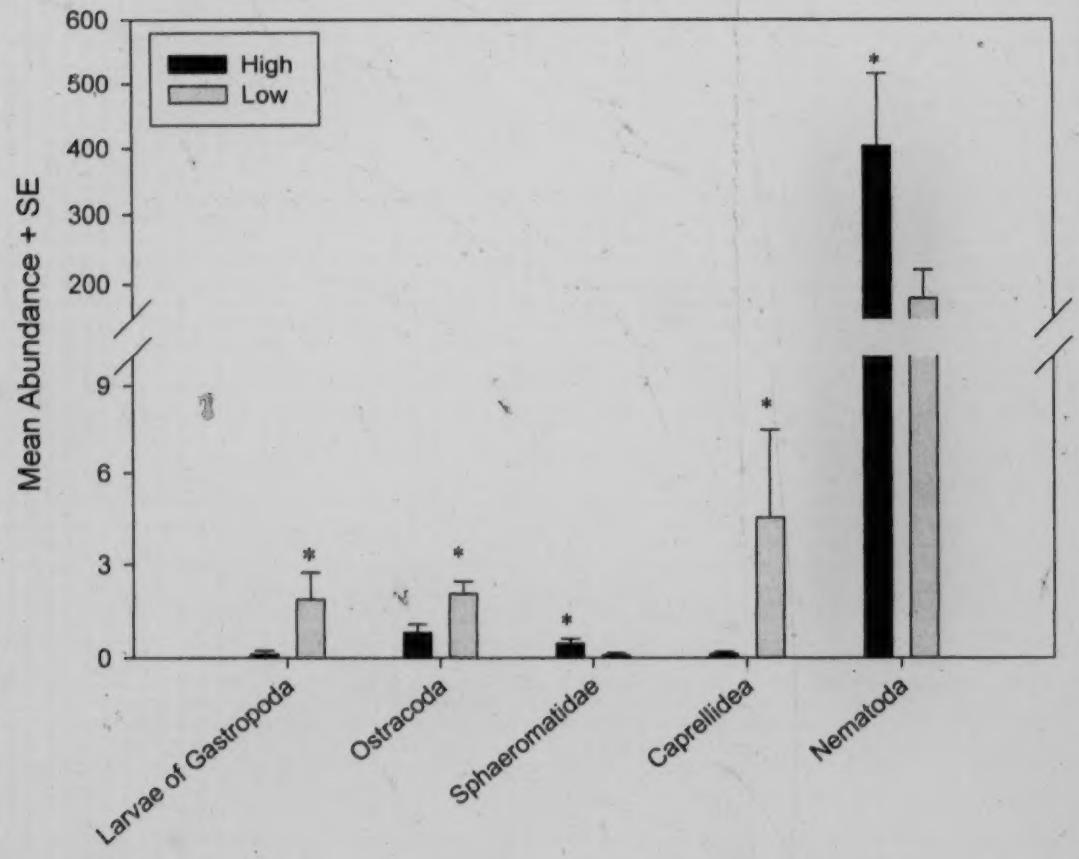


Figure 3-6: Comparison of indicator taxa between high and low transects. All taxa are significantly different between the high and low transects based on t-tests. Asterisk indicate significant at a level of $p \leq 0.05$. Nematode statistical analyses done with log-10 (x+1) transformed data but presented as raw data for comparison. N=30 algal samples per variable.

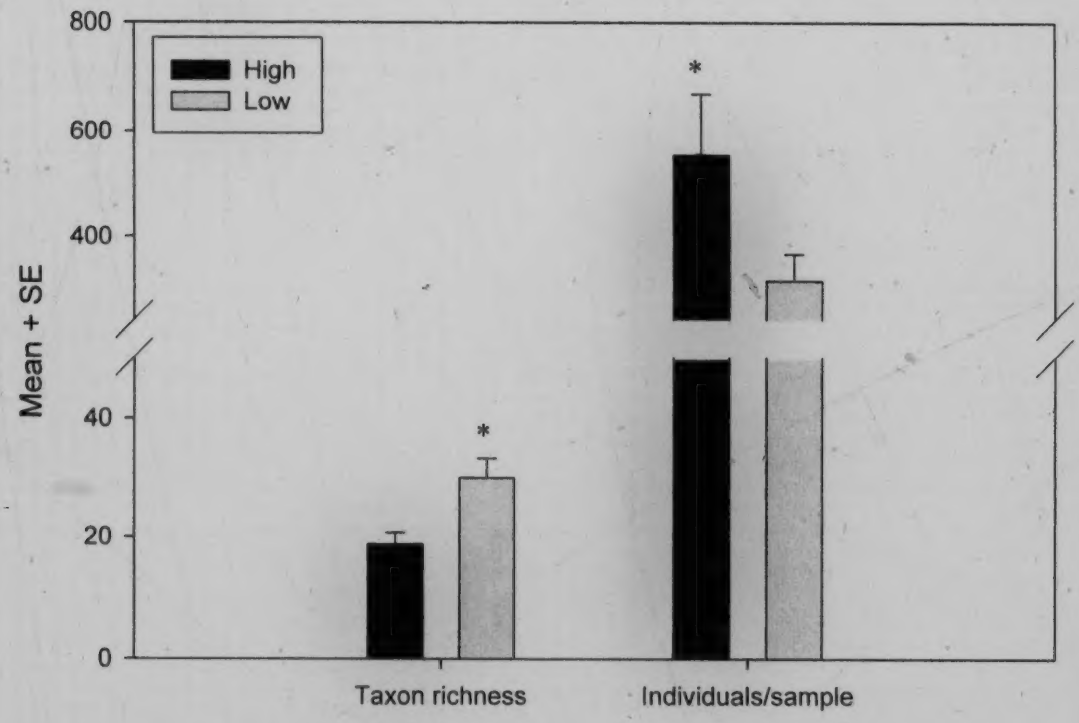
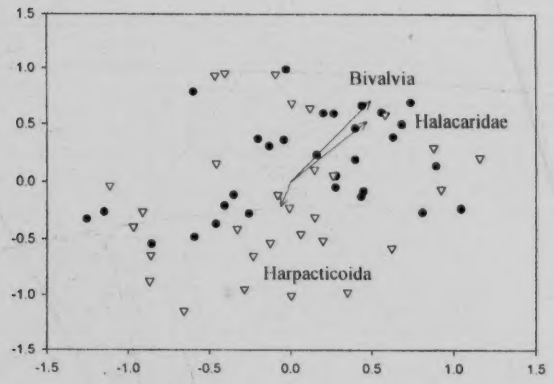
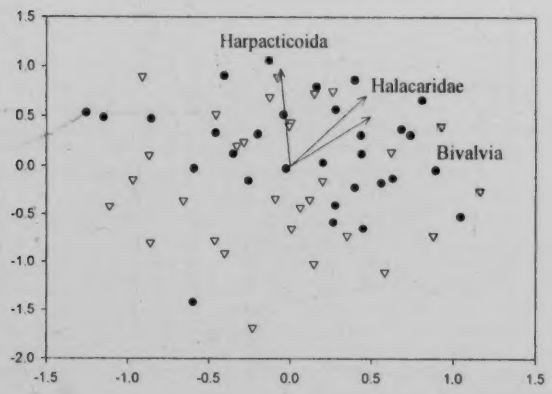


Figure 3-7. Relationship of mean taxon richness and mean individuals/sample for high and low transects. Asterisk indicates significant differences from t-test at a level of $p \leq 0.05$. N=30 algal samples per variable.

A



B



C

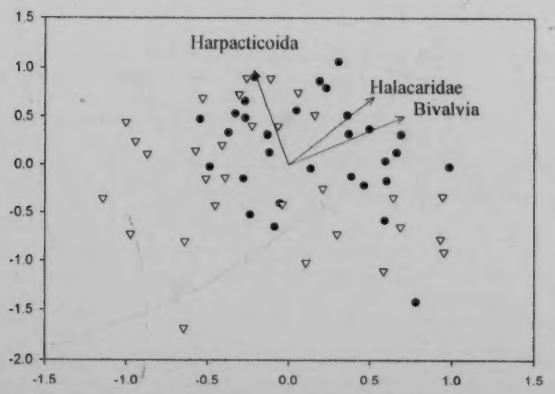


Fig 3-8: Three views of a 3-D semi-strong hybrid multidimensional scaling (SSH-MDS) ordination comparing invertebrate assemblages between exposed (circles, n=30) and submerged samples (triangles, n=30). A) xy axes. B) xz axes. C) yz axes. Nematodes are log 10 (x+1) transformed. Exposed and submerged assemblages are significantly different from each other (ANOSIM $p=0.001$). SSH-MDS stress= 0.15. Vectors shown are significant MCAO $p \leq 0.01$ and PCC r^2 of greater then 0.5.

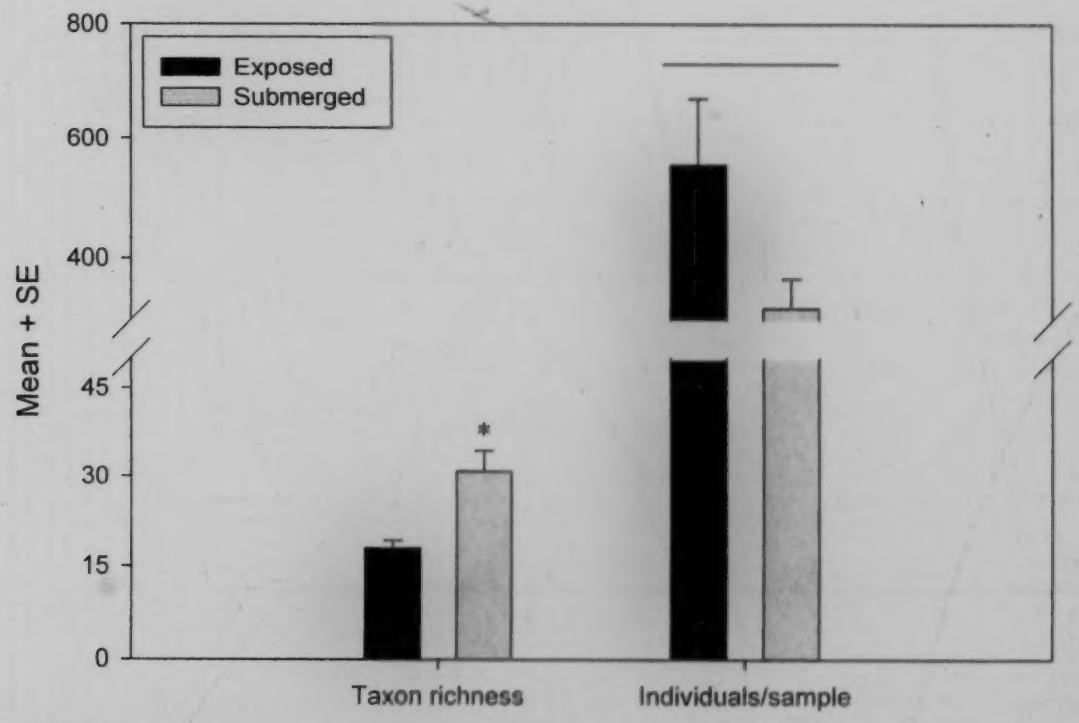


Figure 3-9: Mean taxon richness and mean individuals per sample for the exposed and submerged samples. N=30 algal samples for each grouping variable. Asterisk indicates significant difference from t-tests at a level of $p \leq 0.05$. Line indicates similarity.

Table 3-3: Indicator taxon analysis results and subsequent t-test or Mann-Whitney U test for comparisons of submerged and exposed communities. Bold p-values indicate statistical significance at a level of $p \leq 0.05$. Dagger (†) indicates t-tests, asterisk (*) indicates Mann-Whitney U tests. Nematodes were log 10(x+1) transformed to meet assumptions of normality.

	Indicator Taxon Analysis		**T-/Mann-Whitney U Tests**	
Taxon	IV	p-value	t/z value	p-value
Nereid polychaetes	0.676	**<0.001**	t=4.497†	**<0.001**
Nematoda	0.229	**0.035**	t=2.067†	**0.043**
Nemertea	0.202	**0.033**	z=-1.904*	0.057
Calanoid copepods	0.100	**<0.001**	z=-1.761*	0.078

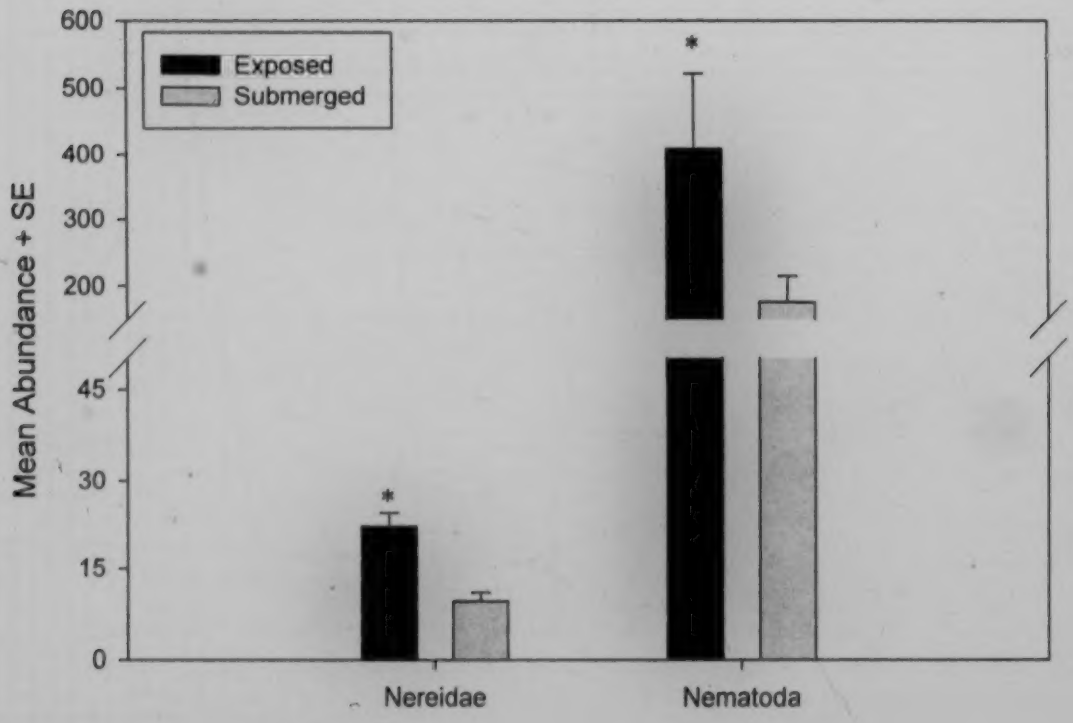


Figure 3-10: Comparison of taxa identified by the ITA indicating exposed and submerged samples. N=30 algal samples for each variable. Asterisk indicates significant difference for t-tests at a level of $p \leq 0.05$.

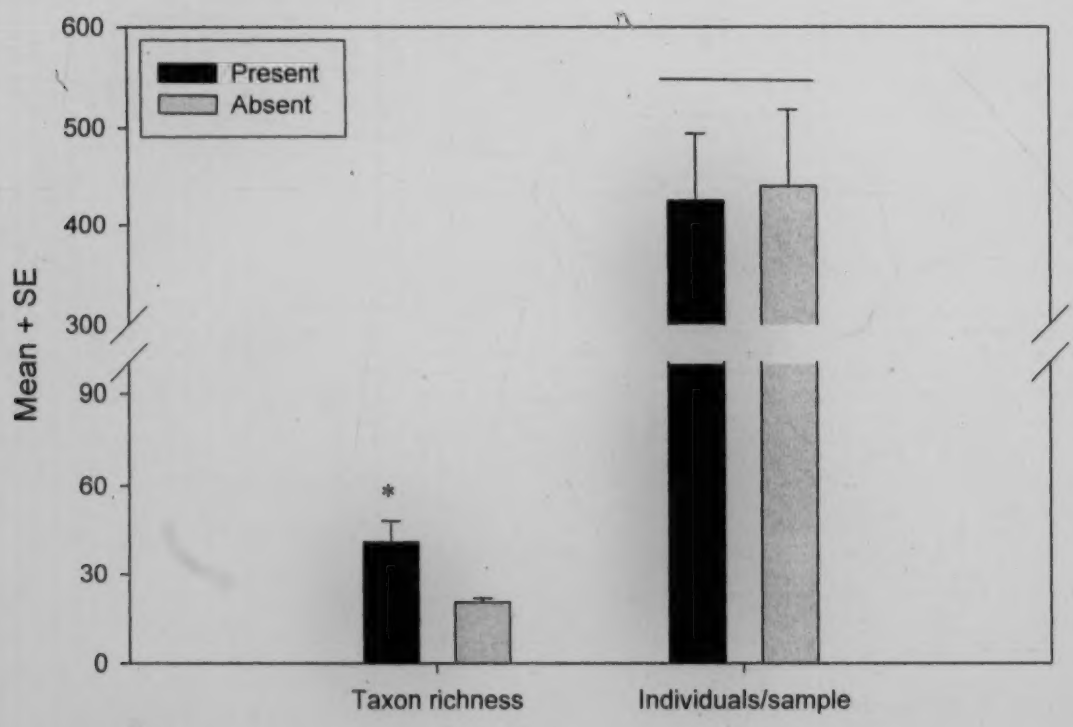


Figure 3-11: Comparison of taxon richness and individuals of samples with and without *Filicrisia franciscana*. Asterisk indicates significant difference for t-tests at a level of $p \leq 0.05$. Line indicates similarity. N=30 algal samples for each variable.

Table 3-4: Indicator taxon analysis results and subsequent t-test or Mann-Whitney U test for samples with and without *Filicrisia franciscana*. Bold p-values indicate statistical significance at a level of $p \leq 0.05$. Dagger (†) indicates t-tests, asterisk (*) indicates Mann-Whitney U tests. Mites were log-10(x+1) transformed to meet assumptions of normality.

	Indicator Taxon Analysis		**T/Mann-Whitney U Tests**	
Taxon	Indicator value	p-value	t/z value	p-value
Halicaridae	IV=0.76	p=**0.002**	t=-4.605	p<**0.001**†
Bivalvia	IV=0.66	p=**0.018**	t=-2.184	p=**0.033**†
Syllidae	IV=0.62	p=**0.010**	z=-3.013	p=**0.003***
Ostracoda	IV=0.54	p=**0.003**	t=-3.001	p=**0.004**†
Caprellidea	IV=0.40	p=**0.004**	z=-2.394	p=**0.017***
Larvae of gastropoda	IV=0.40	p<**0.001**	z=-3.680	p<**0.001***

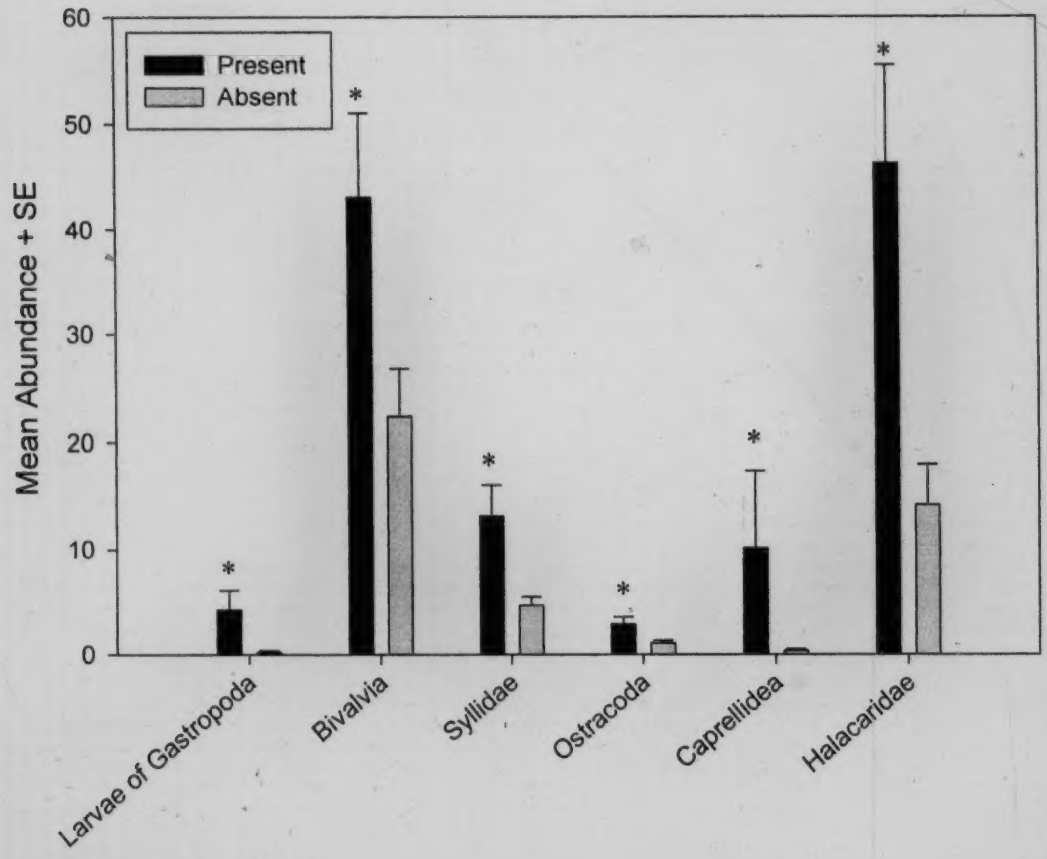


Figure 3-12: Comparison of taxa identified by ITA as being significant for differentiating samples with and without *Filicrisia franciscana*. All differences are significant based on t-tests, asterisk indicates significant difference at a level of $p \leq 0.05$. N=30 algal samples for each variable.

CHAPTER 4: SUMMARY AND CONCLUSIONS

I investigated the roles that geniculate coralline algae (*Corallina vancouveriensis, C. officinalis* and *Bossiella* spp.) play in providing habitat for motile and sessile marine invertebrates. Coralline algae modify the physical structure of rocky habitats and act as foundation species for other organisms. Although not directly experimentally tested, it appears as though coralline algae potentially mitigate environmental stresses such as desiccation during intertidal exposure (Dommasnes 1968), thereby allowing other organisms not normally found on exposed rocky shores to be able to exist there.

The phyletic diversity I found in my subtidal samples was similar to that found in other studies done intertidally in New Zealand and Australia (Hicks 1971, Kelaher et al. 2001, Chapman et al. 2005). There tend to be far more families of polychaetes associated with coralline algae in Australia that I found off Vancouver Island (Kelaher et al. 2001, Chapman et al. 2005). This could be in part due to the difference in biogeographic region and/or to latitudinal gradients in diversity (Gaston 2000). The southeast coast of Australia is around 33°S and my sites in British Columbia are at 49°N. Being 16° closer to a pole than Australia, diversity off Vancouver Island would hypothesized to be comparatively lower. Similar comparisons could not be made for other taxa as polychaetes were the only common taxa identified to family in my study.

I sampled intertidal invertebrate communities inhabiting coralline algae to determine how assemblage structure varied with differences in tidal height and submersion. Using multivariate analyses of variance (ANOSIM), I found no difference in invertebrate assemblage structure between low and high tidal heights; but an indicator taxon analysis (ITA) showed that two taxa (sphaeromatid isopods and nematodes) were

indicative of the high transects and three taxa (caprellid amphipods, ostracods, and gastropod larvae) were indicative of low transects. The lack in overall difference between the high and low transects are in contrast to work done by Kelaher et al. (2001, 2004) in Australia, and many other studies that emphasize the importance of vertical tidal height in delineating invertebrate and algae distribution in the intertidal (Lewis 1964, Raffaelli and Hawkins 1996). However, it is in congruence with work done in Chile and Ireland where no difference was found in molluscan assemblages between tidal heights (Kelaher et al. 2004). A possible explanation why this pattern is so striking in Australia but lacking in other locals is that solar radiation is more intense in Australia so would have greater impact on invertebrates. Such contrasting results demonstrate a need for continued work. It is possible that the coralline algae is effective in retaining water (Padilla 1984) to decrease the impacts of desiccation enough to reduce the observable zoned pattern.

There was a difference in overall assemblage structure between submerged and exposed samples. Nereid polychaetes and nematodes were both significant indicators of exposed samples based on abundance. My results are in contrast to work done by Davenport et al. (1999) who found a greater total abundance of invertebrates associated with submerged samples of *Corallina* sp. in Australia. I found no difference in total abundance, but did, however, find greater taxonomic richness in the submerged samples than the exposed samples, again differing from what Davenport et al. (1999) found, which was no difference. This greater taxonomic richness in submerged samples is not surprising, as physical stresses due to exposure no longer apply while the tide is high.

When comparing my two studies, I found a greater diversity of organisms inhabiting subtidal samples of coralline algae. This is not surprising as rocky subtidal habitats are typically more diverse than adjacent intertidal habitats (Osman and Whitlatch 1998). Taxa found in the subtidal samples that were not present in intertidal collections included opisthobranch molluscs (nudibranchs), pycnogonids, decapod crustaceans, flatworms, and entoprocts. There was also higher familial diversity of polychaetes and isopods. Interestingly, in the intertidal, coralline algae occupies an easily distinguishable band but is found in discrete patches subtidally (pers obs). This could be because competition for space is high in the subtidal (Sebens 1986) due to the reduction in physiological stress or because adequate solid substrate is rarer in the subtidal, much of it being soft sediments.

The presence of erect, branching sessile colonial animals (bryozoans and, in the subtidal study, hydroids) was identified as the strongest predictor of assemblage structure in both the intertidal and subtidal coralline algal turf (Fig. 2-7, Table 3-1, 3-2, and 3-3). This is unexpected for the intertidal assemblages, as vertical height (correlated with increased exposure) is usually described as the dominant force in the intertidal (Lewis 1964, Raffaelli and Hawkins 1996). All invertebrate taxa (except three, see below) were more abundant when in the presence of these branching epifauna. Though very little information exists on the ecology of either of these groups, erect cyclostome bryozoans, and leptomedusan hydrozoans, there are a few possible explanations for this observed pattern. Both the erect bryozoans and the branching hydroids could be acting as additional habitat (niches) for other organisms thus increasing abundance of invertebrates

present. These epibionts may also be passively accumulating detritus and diatoms (Caine 1998) which many of these associated organisms may be feeding on.

Interestingly, nereid polychaetes, calanoid copepods, and idoteid isopods were always more abundant in samples with smaller amounts of either branching bryozoans or hydroids. High densities of these colonial animals may reduce feeding success for the nereids. It is possible that the addition of these substrates acts as refuges for prey (Coull and Wells 1983) and that nereids could have a greater hunting success in more simple habitats where their prey is easier to find (Menge 1978). Nereids create mucus housings from which they feed by sticking together algal fronds (Fauchald and Jumars 1979), so it is conceivable that the bryozoans and hydroids are too brittle for creation of these tubes. Also, nereids and idoteids tended to be the largest organisms found (pers obs) and the smaller branches of the bryozoans and hydrozoans may not have been strong enough to support them.

Underwood et al. (2000) highlight the importance of gathering baseline information such as taxonomic distributions before attempting to evaluate ecological processes. This thesis should be seen as a base from which manipulative experiments can be conducted to better understand the processes driving the distribution patterns of invertebrates on coralline algae. Understanding how branching bryozoans and hydrozoans influence invertebrate assemblages, whether by acting as habitat or by providing food (but most likely a combination), would be an important step. Obviously, the conflict between observations in the literature (Davenport et al. 1999, Hooper and Davenport 2006) and in the results of my studies indicate that more detailed examinations of where invertebrates are found in the intertidal during high tide need to be done. Also,

it would be interesting to determine if there was a difference in subtidal assemblages as one moves seaward, as depth is associated with several changes in abiotic factors such as water flow, light penetration, and sediment loading (Sebens 1986).

Understanding which organisms utilize coralline algae as habitat may have conservation implications. With climate change, increasing levels of oceanic carbon dioxide will cause a reduction in pH levels (McNeil and Matear 2007). This decrease in oceanic pH will have severe implications on organisms, especially those with calcium carbonate structures (Harley et al. 2006). Coralline algae, being composed of magnesian calcites, are though to be especially susceptible to increases in oceanic CO_2 (Feely et al. 2004), and depending on pH changes may suffer reductions in calcification rates of 10-40% (Harley et al. 2006). This reduction in growth could have significant impacts on size and abundance of coralline algae translating to a decrease in habitat for the wide diversity of associated invertebrate fauna. Loss of meiofauna living on the coralline algae could then potentially have bottom-up trophic impacts. Harpacticoid copepods, for example, are a known food source of the commercially important juvenile chum salmon (*Oncorhynus keta* Walbaum) (Sibert et al. 1977). Although there is no currently documented decline in coralline algae populations on rocky shores, it is important to understand the roles of these foundation species whose decline could result in the loss of entire epifaunal communities (Lilley and Schiel 2006). Marine ecologists should take stock of these species-diversifying positive interactions while they still relatively intact.

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Appendix 1: Subtidal Data. Values in brackets are values standardized per dry weight of coralline algae. ^ indicates sampling for presence/absence. * indicates organisms not included in statistical analyses because of too few occurrences. § indicates subsampled nematodes.

			Phylum	Porifera	Cnidaria	Cnidaria
Site	**Depth**	**Replicate**	**Sample**	**Demospongia^**	**Hydrozoa^**	**Anthozoa^**
Aguilar	1	A	A1A	0	1	0
Aguilar	1	B	A1B	0	1	0
Aguilar	1	C	A1C	0	1	1
Aguilar	1	D	A1D	1	0	0
Aguilar	1	E	A1E	1	0	0
Aguilar	2	A	A2A	1	1	0
Aguilar	2	B	A2B	1	0	0
Aguilar	2	C	A2C	1	1	1
Aguilar	2	D	A2D	1	1	0
Aguilar	2	E	A2E	1	1	0
Aguilar	5	A	A5A	1	0	0
Aguilar	5	B	A5B	0	0	0
Aguilar	5	C	A5C	1	1	0
Aguilar	5	D	A5D	1	0	0
Aguilar	5	E	A5E	0	1	0
Dixon	1	A	D1A	1	0	0
Dixon	1	B	D1B	1	0	0
Dixon	1	C	D1C	1	1	0
Dixon	1	D	D1D	1	1	0
Dixon	3	A	D3A	1	1	0
Dixon	3	B	D3B	1	0	0
Dixon	3	C	D3C	1	0	0
Dixon	3	D	D3D	1	1	0
Dixon	3	E	D3E	1	1	0
Dixon	4	A	D4A	1	0	0
Dixon	4	B	D4B	0	1	0
Dixon	4	C	D4C	0	0	0
Dixon	4	D	D4D	1	1	0
Dixon	4	E	D4E	0	0	0
Scotts	1	A	S1A	1	1	0
Scotts	1	B	S1B	1	0	0
Scotts	1	C	S1C	1	1	0
Scotts	1	D	S1D	1	1	0
Scotts	1	E	S1E	1	0	0
Scotts	2	A	S2A	1	1	0
Scotts	2	B	S2B	1	1	0
Scotts	2	C	S2C	1	0	0
Scotts	2	D	S2D	1	0	0
Scotts	2	E	S2E	1	0	1
Scotts	4	A	S4A	1	1	0
Scotts	4	B	S4B	1	1	0
Scotts	4	C	S4C	1	0	1
Scotts	4	D	S4D	1	0	0
Scotts	4	E	S4E	1	1	0

Phylum	Platyhelminthes	Nemertea	Nematoda	Mollusca	Mollusca
Sample	**Polycladida**	**Nemertea**	**Nematoda**	**Gastropoda**	**Nudibranchia**
A1A	0(0.0)	0(0.0)	20(21.8)	1(1.1)	1(1.1)
A1B	0(0.0)	1(1.4)	42(60.0)	3(4.3)	0(0.0)
A1C	0(0.0)	0(0.0)	120(61.3)§	3(1.5)	3(1.5)
A1D	0(0.0)	0(0.0)	188(194.8)	4(4.1)	0(0.0)
A1E	0(0.0)	1(1.6)	31(48.1)	0(0.0)	1(1.6)
A2A	0(0.0)	2(1.6)	30(24.1)	2(1.6)	0(0.0)
A2B	0(0.0)	6(5.7)	56(53.2)	36(34.2)	1(0.9)
A2C	0(0.0)	2(2.8)	295(408.0)	5(6.9)	0(0.0)
A2D	0(0.0)	17(9.9)	292(170.7)§	13(7.6)	4(2.3)
A2E	1(1.0)	5(4.9)	166(161.2)	39(37.9)	0(0.0)
A5A	0(0.0)	0(0.0)	22(48.5)	6(13.2)	0(0.0)
A5B	0(0.0)	0(0.0)	72(138.5)§	3(5.8)	0(0.0)
A5C	0(0.0)	0(0.0)	19(31.5)	0(0.0)	0(0.0)
A5D	0(0.0)	0(0.0)	71(137.3)	3(5.8)	2(3.9)
A5E	0(0.0)	0(0.0)	67(72.0)§	1(1.1)	0(0.0)
D1A	0(0.0)	0(0.0)	94(137.4)	12(17.5)	0(0.0)
D1B	0(0.0)	0(0.0)	75(303.6)§	10(40.5)	0(0.0)
D1C	0(0.0)	0(0.0)	128(318.4)§	26(64.7)	2(5.0)
D1D	0(0.0)	0(0.0)	26(96.3)	4(14.8)	1(3.7)
D3A	0(0.0)	8(11.4)	281(402.0)	20(28.6)	11(15.7)
D3B	2(3.9)	10(19.3)	135(261.1)	10(19.3)	26(50.3)
D3C	4(2.0)	23(11.4)	121(59.9)	9(4.5)	17(8.4)
D3D	0(0.0)	15(15.9)	115(122.2)	6(6.4)	6(6.4)
D3E	1(0.7)	10(6.7)	529(353.1)	99(66.1)	8(5.3)
D4A	0(0.0)	1(1.6)	62(97.9)	3(4.7)	1(1.6)
D4B	0(0.0)	2(2.4)	129(152.7)	5(5.9)	5(5.9)
D4C	0(0.0)	9(10.5)	88(102.4)	3(3.5)	2(2.3)
D4D	0(0.0)	10(17.2)	172(295.5)	3(5.2)	0(0.0)
D4E	0(0.0)	1(2.5)	20(50.1)	2(5.0)	1(2.5)
S1A	0(0.0)	0(0.0)	306(430.3)§	0(0.0)	1(1.4)
S1B	0(0.0)	0(0.0)	34(66.8)	2(3.9)	0(0.0)
S1C	0(0.0)	0(0.0)	671(1582.5)	40(94.3)	0(0.0)
S1D	0(0.0)	0(0.0)	304(403.2)§	34(45.1)	2(2.7)
S1E	1(1.4)	1(1.4)	109(156.6)	3(4.3)	0(0.0)
S2A	0(0.0)	15(12.2)	183(148.4)	50(40.6)	0(0.0)
S2B	0(0.0)	3(3.3)	306(333.0)§	42(45.7)	1(1.1)
S2C	0(0.0)	0(0.0)	400(1069.5)§	12(32.1)	0(0.0)
S2D	4(6.9)	11(19.0)	221(381.7)§	45(77.7)	3(5.2)
S2E	0(0.0)	1(3.8)	617(2373.1)§	40(153.8)	0(0.0)
S4A	0(0.0)	0(0.0)	261(227.2)§	23(20.0)	3(2.6)
S4B	0(0.0)	7(4.0)	381(218.8)§	14(8.0)	0(0.0)
S4C	0(0.0)	0(0.0)	253(309.3)§	2(2.4)	0(0.0)
S4D	0(0.0)	0(0.0)	326(4591.5)	4(56.3)	1(14.1)
S4E	0(0.0)	0(0.0)	130(148.1)	2(2.3)	0(0.0)

Phylum	Mollusca	Mollusca	Annelida	Annelida	Annelida	Annelida
Sample	**Bivalvia**	**Polyplacophora***	**Oligochaeta**	**Syllidae**	**Nereidae**	**Sabellidae**
A1A	21(22.9)	0(0.0)	0(0.0)	17(18.6)	8(8.7)	0(0.0)
A1B	13(18.6)	0(0.0)	0(0.0)	11(15.7)	9(12.9)	0(0.0)
A1C	36(18.4)	0(0.0)	0(0.0)	38(19.4)	2(1.0)	0(0.0)
A1D	58(60.1)	0(0.0)	0(0.0)	61(63.2)	9(9.3)	0(0.0)
A1E	12(18.6)	0(0.0)	0(0.0)	23(35.7)	5(7.8)	1(1.6)
A2A	5(4.0)	0(0.0)	0(0.0)	18(14.5)	11(8.8)	0(0.0)
A2B	30(28.5)	0(0.0)	0(0.0)	70(66.5)	15(14.2)	0(0.0)
A2C	67(92.7)	0(0.0)	0(0.0)	84(116.2)	6(8.3)	3(4.1)
A2D	138(80.7)	1(0.6)	2(1.2)	148(86.5)	13(7.6)	5(2.9)
A2E	77(74.8)	0(0.0)	0(0.0)	139(135.0)	15(14.6)	2(1.9)
A5A	16(35.2)	0(0.0)	0(0.0)	23(50.7)	4(8.8)	3(6.6)
A5B	2(3.8)	0(0.0)	0(0.0)	32(61.5)	5(9.6)	0(0.0)
A5C	5(8.3)	0(0.0)	0(0.0)	4(6.6)	14(23.2)	0(0.0)
A5D	16(30.9)	0(0.0)	0(0.0)	30(58.0)	6(11.6)	0(0.0)
A5E	12(12.9)	0(0.0)	0(0.0)	18(19.3)	13(14.0)	0(0.0)
D1A	22(32.2)	0(0.0)	0(0.0)	34(49.7)	12(17.5)	0(0.0)
D1B	16(64.8)	0(0.0)	0(0.0)	19(76.9)	0(0.0)	0(0.0)
D1C	15(37.3)	0(0.0)	0(0.0)	45(111.9)	0(0.0)	0(0.0)
D1D	7(25.9)	0(0.0)	0(0.0)	10(37.0)	0(0.0)	0(0.0)
D3A	24(34.3)	0(0.0)	0(0.0)	101(144.5)	9(12.9)	0(0.0)
D3B	15(29.0)	0(0.0)	0(0.0)	55(106.4)	3(5.8)	3(5.8)
D3C	11(10.4)	0(0.0)	0(0.0)	169(83.6)	27(13.4)	5(2.5)
D3D	19(20.2)	0(0.0)	0(0.0)	122(129.6)	13(13.8)	2(2.1)
D3E	40(26.7)	0(0.0)	0(0.0)	263(175.6)	7(4.7)	7(4.7)
D4A	7(11.1)	0(0.0)	0(0.0)	12(19.0)	11(17.4)	0(0.0)
D4B	37(43.8)	0(0.0)	0(0.0)	37(43.8)	9(10.7)	0(0.0)
D4C	16(18.6)	0(0.0)	0(0.0)	39(45.4)	29(33.8)	0(0.0)
D4D	33(56.7)	0(0.0)	0(0.0)	21(36.1)	3(5.2)	1(1.7)
D4E	5(12.5)	0(0.0)	0(0.0)	13(32.6)	8(20.1)	0(0.0)
S1A	21(29.5)	0(0.0)	0(0.0)	31(43.6)	4(5.6)	0(0.0)
S1B	0(0.0)	0(0.0)	0(0.0)	13(25.5)	5(9.8)	0(0.0)
S1C	92(217.0)	0(0.0)	0(0.0)	135(318.4)	1(2.4)	7(16.5)
S1D	52(69.0)	0(0.0)	0(0.0)	43(57.0)	1(1.3)	0(0.0)
S1E	53(76.1)	0(0.0)	0(0.0)	34(48.9)	0(0.0)	18(25.9)
S2A	116(94.1)	0(0.0)	0(0.0)	127(103.0)	1(0.8)	2(1.6)
S2B	46(50.1)	0(0.0)	1(1.1)	70(76.2)	6(6.5)	2(2.2)
S2C	39(104.3)	0(0.0)	0(0.0)	38(101.6)	4(10.7)	0(0.0)
S2D	71(122.6)	0(0.0)	0(0.0)	101(174.4)	1(1.7)	0(0.0)
S2E	35(134.6)	0(0.0)	8(30.8)	43(165.4)	2(7.7)	0(0.0)
S4A	98(85.3)	0(0.0)	1(0.9)	120(104.4)	7(6.1)	3(2.6)
S4B	58(33.3)	0(0.0)	0(0.0)	74(42.5)	4(2.3)	2(1.1)
S4C	12(14.7)	0(0.0)	0(0.0)	19(23.2)	11(13.4)	0(0.0)
S4D	56(788.7)	0(0.0)	0(0.0)	47(662.0)	2(28.2)	2(28.2)
S4E	34(38.7)	0(0.0)	0(0.0)	38(43.3)	3(3.4)	5(5.7)

Phylum	Annelida	Annelida	Annelida	Annelida	Annelida
Sample	**Terebellidae**	**Polynoidae**	**Spirorbidae**	**Arabellidae***	**Phyllodocidae**
A1A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
A1B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
A1C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
A1D	1(1.0)	1(1.0)	0(0.0)	0(0.0)	0(0.0)
A1E	0(0.0)	3(4.7)	0(0.0)	0(0.0)	0(0.0)
A2A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
A2B	1(0.9)	1(0.9)	0(0.0)	0(0.0)	0(0.0)
A2C	0(0.0)	3(4.1)	0(0.0)	0(0.0)	0(0.0)
A2D	1(0.6)	3(1.8)	0(0.0)	0(0.0)	3(1.8)
A2E	11(10.7)	1(1.0)	1(1.0)	0(0.0)	0(0.0)
A5A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
A5B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
A5C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
A5D	0(0.0)	2(3.9)	0(0.0)	0(0.0)	0(0.0)
A5E	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
D1A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
D1B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
D1C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
D1D	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
D3A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
D3B	1(1.9)	1(1.9)	0(0.0)	0(0.0)	0(0.0)
D3C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
D3D	0(0.0)	1(1.1)	1(1.1)	0(0.0)	0(0.0)
D3E	33(22.0)	7(4.7)	23(15.4)	0(0.0)	3(2.0)
D4A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
D4B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
D4C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
D4D	1(1.7)	1(1.7)	0(0.0)	0(0.0)	0(0.0)
D4E	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
S1A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
S1B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
S1C	19(44.8)	5(11.8)	0(0.0)	0(0.0)	0(0.0)
S1D	4(5.3)	2(2.7)	0(0.0)	0(0.0)	0(0.0)
S1E	1(1.4)	1(1.4)	0(0.0)	0(0.0)	1(1.4)
S2A	3(2.4)	5(4.1)	0(0.0)	0(0.0)	0(0.0)
S2B	10(10.9)	3(3.3)	1(1.1)	1(1.1)	0(0.0)
S2C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
S2D	5(8.6)	3(5.2)	0(0.0)	0(0.0)	0(0.0)
S2E	4(15.4)	2(7.7)	0(0.0)	0(0.0)	0(0.0)
S4A	8(7.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
S4B	0(0.0)	8(4.6)	0(0.0)	0(0.0)	0(0.0)
S4C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
S4D	11(154.9)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
S4E	5(5.7)	0(0.0)	0(0.0)	0(0.0)	0(0.0)

Phylum	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda
Sample	**Ostracoda**	**Harpacticoida**	**Calanoida**	**Cirripedia**	**Caprellidea**
A1A	31(33.8)	22(24.0)	0(0.0)	0(0.0)	44(48.0)
A1B	31(44.3)	27(38.6)	0(0.0)	0(0.0)	36(51.4)
A1C	79(40.4)	36(18.4)	0(0.0)	0(0.0)	434(221.8)
A1D	39(40.4)	130(134.7)	0(0.0)	0(0.0)	26(26.9)
A1E	15(23.3)	36(55.8)	0(0.0)	0(0.0)	33(51.2)
A2A	18(14.1)	44(35.4)	0(0.0)	0(0.0)	10(8.0)
A2B	66(62.7)	100(95.0)	0(0.0)	0(0.0)	2(1.9)
A2C	314(434.3)	403(557.4)	0(0.0)	0(0.0)	69(95.4)
A2D	410(239.6)	827(483.3)	0(0.0)	1(0.6)	16(9.4)
A2E	166(162.2)	428(415.5)	0(0.0)	0(0.0)	36(35.0)
A5A	28(61.7)	8(17.6)	0(0.0)	0(0.0)	36(79.3)
A5B	21(40.4)	14(26.9)	1(1.9)	2(3.8)	0(0.0)
A5C	11(18.2)	2(3.3)	0(0.0)	0(0.0)	0(0.0)
A5D	50(96.7)	93(179.9)	0(0.0)	0(0.0)	18(34.8)
A5E	45(48.3)	38(40.8)	0(0.0)	0(0.0)	20(21.5)
D1A	42(61.4)	99(144.7)	0(0.0)	0(0.0)	13(19.0)
D1B	4(16.2)	26(105.3)	0(0.0)	0(0.0)	2(8.1)
D1C	38(94.5)	104(258.7)	0(0.0)	0(0.0)	7(17.4)
D1D	5(18.5)	9(33.3)	0(0.0)	0(0.0)	10(37.0)
D3A	90(128.8)	166(237.5)	0(0.0)	4(5.7)	139(198.9)
D3B	107(207.0)	136(263.1)	0(0.0)	0(0.0)	64(123.8)
D3C	282(139.5)	310(153.4)	1(0.5)	1(0.5)	7(3.5)
D3D	103(109.5)	174(184.9)	0(0.0)	0(0.0)	6(6.4)
D3E	409(273.0)	296(197.6)	0(0.0)	1(0.7)	23(15.4)
D4A	9(14.2)	20(31.6)	0(0.0)	0(0.0)	17(26.9)
D4B	5(5.9)	60(71.0)	0(0.0)	0(0.0)	58(68.6)
D4C	30(34.9)	87(101.3)	0(0.0)	0(0.0)	29(33.8)
D4D	142(244.0)	145(249.1)	0(0.0)	0(0.0)	150(257.7)
D4E	11(27.6)	17(42.6)	0(0.0)	0(0.0)	13(32.6)
S1A	36(50.6)	95(133.6)	0(0.0)	0(0.0)	10(14.1)
S1B	3(5.9)	10(19.6)	0(0.0)	0(0.0)	17(33.4)
S1C	196(462.3)	1178(2278.2)	0(0.0)	0(0.0)	32(75.5)
S1D	74(98.1)	197(261.3)	0(0.0)	1(1.3)	19(25.2)
S1E	28(40.2)	163(234.2)	0(0.0)	0(0.0)	15(21.6)
S2A	112(90.8)	404(327.7)	0(0.0)	0(0.0)	69(56.0)
S2B	74(80.5)	237(257.9)	0(0.0)	1(1.1)	115(125.1)
S2C	76(203.2)	313(836.9)	0(0.0)	0(0.0)	94(251.3)
S2D	84(145.1)	313(540.6)	0(0.0)	0(0.0)	59(101.9)
S2E	117(450.0)	411(1580.8)	0(0.0)	0(0.0)	37(142.3)
S4A	63(54.8)	256(222.8)	0(0.0)	0(0.0)	56(48.7)
S4B	92(52.8)	451(259.0)	0(0.0)	0(0.0)	29(16.7)
S4C	13(15.9)	32(39.1)	1(1.2)	0(0.0)	9(11.0)
S4D	57(802.8)	401(5647.9)	0(0.0)	0(0.0)	20(281.7)
S4E	32(36.4)	75(85.4)	0(0.0)	0(0.0)	65(74.0)

Phylum	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda
Sample	**Gammaridea**	**Janaridae**	**Munnidae**	**Jaeropsidae**	**Sphaeromatidae**
A1A	32(34.9)	1(1.1)	0(0.0)	0(0.0)	2(2.2)
A1B	17(24.3)	2(2.9)	0(0.0)	0(0.0)	1(1.4)
A1C	131(66.9)	22(11.2)	2(1.0)	0(0.0)	1(0.5)
A1D	13(13.5)	3(3.1)	3(3.1)	1(1.0)	0(0.0)
A1E	21(32.6)	6(9.3)	0(0.0)	1(1.6)	0(0.0)
A2A	35(28.2)	2(1.6)	1(0.8)	0(0.0)	0(0.0)
A2B	66(62.7)	2(1.9)	3(2.8)	0(0.0)	4(3.8)
A2C	128(177.0)	12(16.6)	6(8.3)	4(5.5)	2(2.8)
A2D	92(42.1)	6(3.6)	8(4.7)	2(1.2)	0(0.0)
A2E	17(16.5)	4(3.9)	10(9.7)	12(11.7)	4(3.9)
A5A	23(50.7)	3(6.6)	0(0.0)	0(0.0)	4(8.8)
A5B	5(9.6)	1(1.9)	0(0.0)	0(0.0)	0(0.0)
A5C	3(5.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
A5D	25(48.4)	4(7.7)	0(0.0)	0(0.0)	0(0.0)
A5E	9(9.7)	0(0.0)	0(0.0)	0(0.0)	1(1.1)
D1A	9(10.2)	3(4.4)	0(0.0)	0(0.0)	0(0.0)
D1B	1(4.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
D1C	28(69.7)	1(2.5)	3(7.5)	0(0.0)	0(0.0)
D1D	4(14.8)	1(3.7)	0(0.0)	0(0.0)	0(0.0)
D3A	103(147.4)	13(18.6)	20(28.6)	2(2.9)	7(10.0)
D3B	122(236.0)	20(38.7)	11(21.3)	0(0.0)	1(1.9)
D3C	191(94.5)	20(9.9)	8(4.0)	3(1.5)	6(3.0)
D3D	30(31.9)	5(5.3)	4(4.3)	9(9.6)	0(0.0)
D3E	152(101.5)	69(46.1)	11(7.3)	9(6.0)	2(1.3)
D4A	9(14.2)	1(1.6)	0(0.0)	0(0.0)	0(0.0)
D4B	28(33.1)	9(10.7)	2(2.4)	0(0.0)	3(3.6)
D4C	20(23.3)	3(3.5)	0(0.0)	0(0.0)	6(7.0)
D4D	61(104.8)	13(22.3)	1(1.7)	0(0.0)	6(10.3)
D4E	2(5.0)	2(5.0)	0(0.0)	0(0.0)	3(7.5)
S1A	15(21.1)	4(5.6)	0(0.0)	0(0.0)	1(1.4)
S1B	11(21.6)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
S1C	121(285.4)	29(63.7)	0(0.0)	2(4.7)	0(0.0)
S1D	64(84.9)	12(15.9)	0(0.0)	3(4.0)	0(0.0)
S1E	38(54.6)	5(7.2)	0(0.0)	6(8.6)	0(0.0)
S2A	297(240.9)	34(27.6)	12(9.7)	18(14.6)	0(0.0)
S2B	352(383.0)	14(15.2)	5(5.4)	1(1.1)	3(3.3)
S2C	247(660.4)	21(56.1)	3(8.0)	1(2.7)	0(0.0)
S2D	138(238.3)	5(8.6)	2(3.5)	2(3.5)	0(0.0)
S2E	471(1811.5)	18(69.2)	15(57.7)	9(34.6)	0(0.0)
S4A	72(62.7)	30(26.1)	1(0.9)	6(5.2)	0(0.0)
S4B	73(41.9)	19(10.9)	3(1.7)	0(0.0)	0(0.0)
S4C	23(28.1)	3(3.7)	0(0.0)	0(0.0)	0(0.0)
S4D	5(70.4)	13(183.1)	2(28.2)	0(0.0)	0(0.0)
S4E	102(116.2)	6(6.8)	5(5.7)	0(0.0)	0(0.0)

Phylum	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda
Sample	**Anthuridae***	**Idoteidae**	**Paratanaidae**	**Tanaidae**	**Halacaridae**
A1A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	23(25.1)
A1B	0(0.0)	1(1.4)	0(0.0)	0(0.0)	18(25.7)
A1C	0(0.0)	1(0.5)	0(0.0)	0(0.0)	35(17.9)
A1D	0(0.0)	0(0.0)	1(1.0)	0(0.0)	18(18.7)
A1E	0(0.0)	0(0.0)	0(0.0)	1(1.6)	14(21.7)
A2A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	28(22.5)
A2B	0(0.0)	0(0.0)	1(0.9)	0(0.0)	38(36.1)
A2C	0(0.0)	0(0.0)	2(2.8)	0(0.0)	80(110.7)
A2D	3(1.8)	0(0.0)	11(6.4)	0(0.0)	240(140.3)
A2E	0(0.0)	0(0.0)	1(1.0)	0(0.0)	152(147.6)
A5A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	18(39.6)
A5B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	21(40.4)
A5C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	3(5.0)
A5D	0(0.0)	0(0.0)	0(0.0)	0(0.0)	49(94.8)
A5E	0(0.0)	0(0.0)	0(0.0)	0(0.0)	42(45.1)
D1A	0(0.0)	0(0.0)	1(1.5)	0(0.0)	76(111.1)
D1B	0(0.0)	0(0.0)	1(4.0)	0(0.0)	26(105.3)
D1C	0(0.0)	0(0.0)	0(0.0)	1(2.5)	33(82.1)
D1D	0(0.0)	1(3.7)	0(0.0)	0(0.0)	23(85.2)
D3A	0(0.0)	0(0.0)	5(7.2)	1(1.4)	186(266.1)
D3B	0(0.0)	0(0.0)	2(3.9)	0(0.0)	121(234.0)
D3C	0(0.0)	0(0.0)	8(4.0)	0(0.0)	129(63.8)
D3D	0(0.0)	0(0.0)	1(1.1)	0(0.0)	180(191.3)
D3E	0(0.0)	0(0.0)	1(0.7)	0(0.0)	427(285.0)
D4A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	40(63.2)
D4B	0(0.0)	1(1.2)	0(0.0)	0(0.0)	169(200.0)
D4C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	103(119.9)
D4D	0(0.0)	0(0.0)	3(5.2)	0(0.0)	71(122.0)
D4E	0(0.0)	0(0.0)	0(0.0)	0(0.0)	15(37.6)
S1A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	45(63.3)
S1B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	13(25.5)
S1C	0(0.0)	0(0.0)	11(25.9)	0(0.0)	310(731.1)
S1D	0(0.0)	0(0.0)	0(0.0)	0(0.0)	74(98.1)
S1E	0(0.0)	0(0.0)	3(4.3)	0(0.0)	36(51.7)
S2A	0(0.0)	0(0.0)	1(0.8)	0(0.0)	159(129.0)
S2B	1(1.1)	0(0.0)	0(0.0)	0(0.0)	99(107.7)
S2C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	91(243.3)
S2D	0(0.0)	0(0.0)	3(5.2)	2(3.5)	173(298.8)
S2E	0(0.0)	0(0.0)	3(11.5)	0(0.0)	97(373.1)
S4A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	133(115.8)
S4B	0(0.0)	0(0.0)	1(0.6)	1(0.6)	223(128.1)
S4C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	51(62.3)
S4D	0(0.0)	0(0.0)	2(28.2)	0(0.0)	79(1112.7)
S4E	0(0.0)	0(0.0)	0(0.0)	0(0.0)	72(82.0)

Phylum	Arthropoda	Echinodermata	Entoprocta		
Sample	**Pycnogonida**	**Ophiuroidea***	**Entoprocta^**	**Total**	**Taxon count**
A1A	0(0.0)	0(0.0)	0	224(246.7)	14(17.5)
A1B	0(0.0)	0(0.0)	1	214(308.6)	16(25.7)
A1C	0(0.0)	0(0.0)	0	945(483.9)	17(9.7)
A1D	0(0.0)	0(0.0)	0	556(579.3)	16(19.7)
A1E	0(0.0)	0(0.0)	1	205(322.5)	17(31.0)
A2A	0(0.0)	0(0.0)	1	208(169.8)	15(14.5)
A2B	0(0.0)	0(0.0)	1	499(476.7)	19(20.9)
A2C	0(0.0)	0(0.0)	0	1487(2060.9)	20(31.8)
A2D	0(0.0)	0(0.0)	0	2237(1309.2)	25(16.4)
A2E	0(0.0)	0(0.0)	1	1289(1254.4)	23(25.2)
A5A	0(0.0)	0(0.0)	0	194(433.9)	13(35.2)
A5B	0(0.0)	0(0.0)	0	179(348.1)	12(26.9)
A5C	0(0.0)	0(0.0)	0	62(107.8)	9(19.9)
A5D	0(0.0)	0(0.0)	1	370(721.5)	14(32.9)
A5E	0(0.0)	0(0.0)	1	268(291.1)	13(17.2)
D1A	0(0.0)	0(0.0)	0	415(612.6)	12(23.4)
D1B	0(0.0)	0(0.0)	0	180(736.8)	10(48.6)
D1C	0(0.0)	0(0.0)	0	432(1079.6)	14(39.8)
D1D	0(0.0)	0(0.0)	1	103(338.9)	14(59.3)
D3A	1(1.4)	0(0.0)	0	1193(1709.6)	22(34.3)
D3B	0(0.0)	0(0.0)	0	845(1640.2)	20(44.5)
D3C	0(0.0)	0(0.0)	0	1364(676.4)	22(12.4)
D3D	0(0.0)	0(0.0)	1	814(869.3)	21(26.6)
D3E	4(2.7)	7(4.7)	0	2446(1634.8)	28(20.7)
D4A	0(0.0)	0(0.0)	0	193(308.1)	13(23.7)
D4B	0(0.0)	0(0.0)	1	561(667.5)	18(24.9)
D4C	0(0.0)	0(0.0)	0	464(542.5)	14(18.6)
D4D	1(1.7)	0(0.0)	1	840(1448.5)	21(41.2)
D4E	0(0.0)	0(0.0)	0	113(285.7)	14(37.6)
S1A	0(0.0)	0(0.0)	0	570(807.3)	13(23.9)
S1B	0(0.0)	0(0.0)	0	108(220.0)	9(25.5)
S1C	1(2.4)	1(2.4)	1	2852(6733.5)	21(56.6)
S1D	1(1.3)	0(0.0)	1	898(1195.0)	19(29.2)
S1E	0(0.0)	0(0.0)	0	516(745.7)	18(30.2)
S2A	0(0.0)	0(0.0)	1	1610(1309.0)	20(19.5)
S2B	0(0.0)	0(0.0)	0	1395(1522.3)	25(31.6)
S2C	0(0.0)	0(0.0)	1	1340(3590.9)	14(45.5)
S2D	0(0.0)	0(0.0)	1	1247(2158.9)	21(41.5)
S2E	0(0.0)	0(0.0)	1	1933(7446.2)	21(92.3)
S4A	0(0.0)	0(0.0)	1	1143(997.4)	19(19.1)
S4B	0(0.0)	0(0.0)	1	1442(830.6)	19(13.2)
S4C	0(0.0)	0(0.0)	1	431(531.8)	14(22.0)
S4D	0(0.0)	0(0.0)	0	1028(14535.2)	16(281.7)
S4E	1(1.1)	0(0.0)	1	557(659.5)	17(21.6)

Phylum	Rhodophyta	Rhodophyta	Ectoprocta	Ectoprocta
Sample	**Corallinacea (g)**	**Dominant species of Corallinacea in sample**	***Flustrellidra* (g)**	**Encrusting bryozoa (g)**
A1A	0.916	*Bosseilla* spp.	0	0.022
A1B	0.700	*Bosseilla* spp.	0	0
A1C	1.957	*Bosseilla* spp.	0	0.277
A1D	0.965	*Bosseilla* spp.	0	0.022
A1E	0.645	*Bosseilla* spp.	0	0.371
A2A	1.243	*Bosseilla* spp.	0	0.037
A2B	1.053	*Bosseilla* spp.	0	0.101
A2C	0.723	*Corallina officinalis*	0	0.478
A2D	1.711	*Bosseilla* spp.	0	0.007
A2E	1.030	*Bosseilla* spp.	0	0.017
A5A	0.454	*Bosseilla* spp.	0	0.228
A5B	0.520	*Bosseilla* spp.	0	0.604
A5C	0.603	*Bosseilla* spp.	0	0.169
A5D	0.517	*Bosseilla* spp.	0	0.153
A5E	0.931	*Bosseilla* spp.	0	0.106
D1A	0.684	*C. officinalis*	0.023	0
D1B	0.247	*C. officinalis*	0	0
D1C	0.402	*C. officinalis*	0	0
D1D	0.270	*C. officinalis*	0	0.001
D3A	0.699	*C. officinalis*	0	0.584
D3B	0.517	*C. officinalis*	0	0
D3C	2.021	*C. officinalis*	0	0.179
D3D	0.941	*C. officinalis*	0.002	0.529
D3E	1.498	*C. officinalis*	0	0.215
D4A	0.633	*C. officinalis*	0.013	0.261
D4B	0.845	*C. officinalis*	0.031	0
D4C	0.859	*C. officinalis*	0	0.455
D4D	0.582	*C. officinalis*	0	0.037
D4E	0.399	*C. officinalis*	0	0.026
S1A	0.711	*C. officinalis*	0.070	0
S1B	0.509	*C. officinalis*	0.002	0.134
S1C	0.424	*C. officinalis*	0.117	0
S1D	0.754	*Bosseilla* spp.	0.015	0
S1E	0.696	*C. officinalis*	0	0
S2A	1.233	*Bosseilla* spp.	0	0
S2B	0.919	*Bosseilla* spp.	0	0
S2C	0.374	*C. officinalis*	0	0
S2D	0.579	*Bosseilla* spp.	0	0.132
S2E	0.260	*C. officinalis*	0	0
S4A	1.149	*C. officinalis*	0	0.164
S4B	1.741	*Bosseilla* spp.	0.081	0.129
S4C	0.818	*Bosseilla* spp.	0.197	0.271
S4D	0.071	*C. officinalis*	0.056	0
S4E	0.878	*C. officinalis*	0	0

Phylum	Ectoprocta	Cnidaria
Sample	**Erect bryozoa (g)**	***Aglaophenia* (g)**
A1A	0	0.007
A1B	0	0.005
A1C	0	0.155
A1D	0.153	0.007
A1E	0.004	0.006
A2A	0.001	0.003
A2B	0.043	0.002
A2C	0.118	0.001
A2D	0.082	0.014
A2E	0.438	0.006
A5A	0.035	0.010
A5B	0.001	0
A5C	0.001	0
A5D	0.044	0
A5E	0.001	0
D1A	0.157	0
D1B	0.028	0
D1C	0.084	0
D1D	0.018	0
D3A	0.144	0.154
D3B	0.091	0.071
D3C	0.129	0.048
D3D	0	0.016
D3E	0.084	0.039
D4A	0	0.010
D4B	0.057	0.027
D4C	0.014	0.016
D4D	0.046	0.004
D4E	0.01	0.006
S1A	0.034	0.013
S1B	0	0.006
S1C	0.577	0.013
S1D	0.172	0.002
S1E	0.177	0.005
S2A	0.438	0.004
S2B	0.222	0.010
S2C	0.071	0
S2D	0.317	0.043
S2E	0.127	0.001
S4A	0.402	0.032
S4B	0.050	0.004
S4C	0.001	0
S4D	0	0.255
S4E	0.168	0.017

Appendix 2: Taxon counts for intertidal site Aguilar Point. Values in brackets are values standardized for dry algal weight. ^ indicates sampling for presence/absence. * indicates organisms not included in statistical analyses because of too few occurrences. § indicates nematode subsampling.

				Phylum	Porifera	Cnidaria	Nemertea	Mollusca	Mollusca	Mollusca	Mollusca
Site	**Transect**	**Exposure**	**Replicate**	**Sample**	**Porifera^**	**Hydroida^**	**Nemertea**	**Polyplacophora**	**Larvae of gastropoda**	**Gastropoda**	**Bivalvia**
Aguilar	High	Exposed	A	**AHE-A**	0	1	0(0.0)	0(0.0)	0(0.0)	0(0.0)	52(53.9)
Aguilar	High	Exposed	C	**AHE-C**	0	0	1(1.6)	0(0.0)	0(0.0)	0(0.0)	2(3.3)
Aguilar	High	Exposed	G	**AHE-G**	0	1	1(1.5)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
Aguilar	High	Exposed	H	**AHE-H**	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	8(9.9)
Aguilar	High	Exposed	J	**AHE-J**	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	16(18.4)
Aguilar	High	Submerged	A	**AHS-A**	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	7(6.9)
Aguilar	High	Submerged	B	**AHS-B**	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	34(79.3)
Aguilar	High	Submerged	C	**AHS-C**	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	7(17.4)
Aguilar	High	Submerged	G	**AHS-G**	0	1	0(0.0)	0(0.0)	0(0.0)	1(2.3)	4(9.3)
Aguilar	High	Submerged	I	**AHS-I**	1	1	0(0.0)	1(3.6)	1(3.6)	0(0.0)	7(25.2)
Aguilar	Low	Exposed	A	**ALE-A**	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	4(7.8)
Aguilar	Low	Exposed	C	**ALE-C**	0	1	1(2.4)	0(0.0)	8(19.5)	11(26.8)	37(90.2)
Aguilar	Low	Exposed	E	**ALE-E**	0	1	1(1.3)	0(0.0)	7(9.4)	3(4.0)	57(76.7)
Aguilar	Low	Exposed	G	**ALE-G**	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(4.0)
Aguilar	Low	Exposed	I	**ALE-I**	0	0	0(0.0)	0(0.0)	3(7.6)	1(2.5)	6(15.2)
Aguilar	Low	Submerged	A	**ALS-A**	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	9(12.6)
Aguilar	Low	Submerged	B	**ALS-B**	0	0	0(0.0)	0(0.0)	0(0.0)	1(1.9)	8(15.1)
Aguilar	Low	Submerged	C	**ALS-C**	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(5.5)
Aguilar	Low	Submerged	E	**ALS-E**	0	1	0(0.0)	0(0.0)	0(0.0)	1(2.7)	6(16.3)
Aguilar	Low	Submerged	I	**ALS-I**	0	0	0(0.0)	0(0.0)	1(5.7)	0(0.0)	3(17.1)

Phylum	Annelida	Annelida	Annelida	Annelida	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda
Sample	Oligochaeta	Nereidae	Syllidae	Sabellidae *	Ostracods	Harpacticoid copepods	Calanoid copepods	Naupliar larvae	Caprellid amphipods	Gammarid Amphipods
AHE-A	0(0.0)	33(34.2)	12(12.4)	0(0.0)	2(2.1)	111(115.0)	0(0.0)	51(52.8)	2(2.1)	12(12.4)
AHE-C	0(0.0)	32(52.1)	0(0.0)	0(0.0)	1(1.6)	16(26.1)	0(0.0)	11(17.9)	0(0.0)	1(1.6)
AHE-G	0(0.0)	20(29.9)	3(4.5)	0(0.0)	0(0.0)	45(67.3)	0(0.0)	20(29.9)	0(0.0)	0(0.0)
AHE-H	0(0.0)	18(22.3)	0(0.0)	0(0.0)	1(1.2)	58(71.8)	0(0.0)	37(45.8)	0(0.0)	3(3.7)
AHE-J	0(0.0)	27(31.1)	3(3.5)	0(0.0)	2(2.3)	74(85.2)	0(0.0)	87(100.1)	0(0.0)	0(0.0)
AHS-A	0(0.0)	1(1.0)	0(0.0)	0(0.0)	0(0.0)	14(13.7)	0(0.0)	2(2.0)	0(0.0)	0(0.0)
AHS-B	0(0.0)	1(2.3)	2(4.7)	0(0.0)	0(0.0)	3(7.0)	1(2.3)	0(0.0)	0(0.0)	0(0.0)
AHS-C	0(0.0)	1(2.5)	0(0.0)	0(0.0)	0(0.0)	3(7.5)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
AHS-G	0(0.0)	3(6.9)	5(11.6)	0(0.0)	0(0.0)	5(11.6)	0(0.0)	1(2.3)	0(0.0)	0(0.0)
AHS-I	0(0.0)	3(10.8)	3(10.8)	1(3.6)	0(0.0)	6(21.6)	0(0.0)	3(10.8)	0(0.0)	2(7.2)
ALE-A	0(0.0)	10(19.5)	3(5.8)	0(0.0)	2(3.9)	10(19.5)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
ALE-C	0(0.0)	10(24.4)	3(7.3)	0(0.0)	1(2.4)	52(126.8)	0(0.0)	2(4.9)	0(0.0)	1(2.4)
ALE-E	0(0.0)	12(16.2)	11(14.8)	0(0.0)	2(2.7)	81(109.0)	0(0.0)	3(4.0)	2(2.7)	11(14.8)
ALE-G	0(0.0)	5(20.1)	0(0.0)	0(0.0)	1(4.0)	10(40.2)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
ALE-I	0(0.0)	12(30.4)	2(5.1)	0(0.0)	2(5.1)	25(63.3)	0(0.0)	5(12.7)	0(0.0)	1(2.5)
ALS-A	1(1.8)	11(19.9)	2(3.6)	0(0.0)	2(3.6)	8(14.4)	0(0.0)	5(9.0)	0(0.0)	0(0.0)
ALS-B	0(0.0)	2(3.8)	0(0.0)	0(0.0)	0(0.0)	3(5.7)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
ALS-C	0(0.0)	0(0.0)	4(22.1)	0(0.0)	0(0.0)	2(11.0)	0(0.0)	1(5.5)	0(0.0)	1(5.5)
ALS-E	0(0.0)	6(16.3)	4(10.9)	0(0.0)	0(0.0)	35(95.4)	0(0.0)	22(59.9)	1(2.7)	1(2.7)
ALS-I	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(5.7)	4(22.9)	0(0.0)	6(34.3)	0(0.0)	0(0.0)

Phylum	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Nematoda		
Sample	Idoteidae *	Sphaeromatidae	Janiridae	Munnidae *	Halicarid Mites	Chironomid	Nematode	Individuals per sample	Taxon Richness
AHE-A	0(0.0)	1(1.0)	1(1.0)	0(0.0)	7(7.3)	2(2.1)	322(333.7)	610(632.1)	15(15.5)
AHE-C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	2(3.3)	1(1.6)	556(905.5)§	624(1016.3)	11(17.9)
AHE-G	1(1.5)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	156(233.2)	248(370.7)	9(13.5)
AHE-H	0(0.0)	3(3.7)	0(0.0)	0(0.0)	5(6.2)	1(1.2)	110(136.1)	245(303.2)	11(13.6)
AHE-J	0(0.0)	0(0.0)	0(0.0)	0(0.0)	3(3.5)	0(0.0)	556(639.8)§	769(884.9)	9(10.4)
AHS-A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	2(2.0)	2(2.0)	38(37.3)	67(65.7)	8(7.8)
AHS-B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	5(11.7)	1(2.3)	16(37.3)	65(151.5)	10(23.3)
AHS-C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	2(5.0)	0(0.0)	44(109.5)	58(144.3)	6(14.9)
AHS-G	0(0.0)	0(0.0)	0(0.0)	0(0.0)	3(6.9)	0(0.0)	9(20.8)	33(76.4)	10(23.1)
AHS-I	0(0.0)	0(0.0)	0(0.0)	0(0.0)	7(25.2)	0(0.0)	52(187.1)	90(323.7)	15(54.0)
ALE-A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	42(81.7)	72(140.1)	7(13.6)
ALE-C	0(0.0)	1(2.4)	0(0.0)	0(0.0)	39(95.1)	1(2.4)	90(219.5)	260(634.1)	17(41.5)
ALE-E	0(0.0)	0(0.0)	0(0.0)	0(0.0)	49(65.9)	1(1.3)	340(457.6)	583(784.7)	17(22.9)
ALE-G	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(4.0)	0(0.0)	26(104.4)	45(180.7)	7(28.1)
ALE-I	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(2.5)	0(0.0)	13(32.9)	72(182.3)	12(30.4)
ALS-A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	3(5.4)	0(0.0)	52(93.9)	92(166.1)	10(18.1)
ALS-B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	2(3.8)	0(0.0)	11(20.8)	28(52.8)	7(13.2)
ALS-C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	6(33.1)	0(0.0)	13(71.8)	30(165.7)	9(49.7)
ALS-E	0(0.0)	0(0.0)	0(0.0)	0(0.0)	6(16.3)	0(0.0)	10(27.2)	94(256.1)	12(32.7)
ALS-I	0(0.0)	0(0.0)	0(0.0)	0(0.0)	2(11.4)	0(0.0)	5(28.6)	24(137.1)	9(51.4)

Phylum	Rhodophyta	Rhodophyta	Ectoprocta	Ectoprocta	Ectoprocta	
Sample	Weight of *Corallinacea* (g)	Dominant species of Corallinacea in sample	Weight of *Flustrellidra* (g)	Weight of calcified bryozoa (g)	Weight of *Filicrisia* (g)	Total weight
AHE-A	0.965	*Corallina vancouveriensis*	0	0.025	0	0.99
AHE-C	0.614	*C. vancouveriensis*	0	0.008	0	0.622
AHE-G	0.669	*C. vancouveriensis*	0	0.0009	0	0.6699
AHE-H	0.808	*C. vancouveriensis*	0	0.016	0	0.824
AHE-J	0.869	*C. vancouveriensis*	0	0.0009	0	0.8699
AHS-A	1.02	*C. vancouveriensis*	0	0.017	0	1.037
AHS-B	0.429	*C. vancouveriensis*	0.0009	0.005	0	0.4349
AHS-C	0.402	*C. vancouveriensis*	0	0.006	0	0.408
AHS-G	0.432	*C. vancouveriensis*	0	0.007	0	0.439
AHS-I	0.278	*C. vancouveriensis*	0	0.011	0.0009	0.2899
ALE-A	0.514	*C. vancouveriensis*	0	0.002	0	0.516
ALE-C	0.41	*C. vancouveriensis*	0	0.0009	0.0009	0.4118
ALE-E	0.743	*C. vancouveriensis*	0	0.041	0.0009	0.7849
ALE-G	0.249	*C. vancouveriensis*	0	0.0009	0	0.2499
ALE-I	0.395	*C. vancouveriensis*	0	0.001	0	0.396
ALS-A	0.554	*C. vancouveriensis*	0	0.028	0	0.582
ALS-B	0.53	*C. vancouveriensis*	0	0.0009	0	0.5309
ALS-C	0.181	*Bossiella* spp.	0	0.062	0.0009	0.2439
ALS-E	0.367	*C. vancouveriensis*	0	0.024	0	0.391
ALS-I	0.175	*C. vancouveriensis*	0	0.006	0.0009	0.1819

Appendix 3: Taxon counts for intertidal site Brady's Beach. Values in brackets are values standardized for dry algal weight. ^ indicates sampling for presence/absence. * indicates organisms not included in statistical analyses because of too few occurrences. § indicates nematode subsampling.

				Phylum	Porifera	Cnidaria	Nemertea	Mollusca	Mollusca	Mollusca	Mollusca
Site	Transect	Exposure	Replicate	Sample	Porifera^	Hydroida^	Nemertea	Polyplacophora	Larvae of gastropods	Gastropods	Bivalvia
Brady	High	Exposed	A	BHE-A	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	13(20.7)
Brady	High	Exposed	B	BHE-B	1	0	0(0.0)	1(0.7)	0(0.0)	2(1.5)	142(106.3)
Brady	High	Exposed	F	BHE-F	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	6(8.9)
Brady	High	Exposed	G	BHE-G	0	1	0(0.0)	1(1.1)	0(0.0)	1(1.1)	47(50.0)
Brady	High	Exposed	H	BHE-H	0	0	0(0.0)	1(0.9)	0(0.0)	0(0.0)	5(4.5)
Brady	High	Submerged	A	BHS-A	0	0	0(0.0)	0(0.0)	0(0.0)	1(4.4)	11(48.2)
Brady	High	Submerged	B	BHS-B	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	14(25.8)
Brady	High	Submerged	D	BHS-D	0	0	0(0.0)	0(0.0)	0(0.0)	1(2.4)	17(40.5)
Brady	High	Submerged	I	BHS-I	0	0	1(1.4)	0(0.0)	0(0.0)	0(0.0)	20(29.0)
Brady	High	Submerged	J	BHS-J	0	0	0(0.0)	0(0.0)	0(0.0)	1(2.1)	7(14.4)
Brady	Low	Exposed	B	BLE-B	0	0	0(0.0)	0(0.0)	1(1.9)	0(0.0)	0(0.0)
Brady	Low	Exposed	D	BLE-D	0	1	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
Brady	Low	Exposed	G	BLE-G	0	1	1(1.2)	1(1.2)	0(0.0)	0(0.0)	8(9.3)
Brady	Low	Exposed	H	BLE-H	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	5(13.9)
Brady	Low	Exposed	J	BLE-J	0	0	1(1.8)	0(0.0)	0(0.0)	0(0.0)	1(1.8)
Brady	Low	Submerged	A	BLS-A	0	1	0(0.0)	0(0.0)	0(0.0)	0(0.0)	12(53.8)
Brady	Low	Submerged	B	BLS-B	0	1	0(0.0)	0(0.0)	0(0.0)	1(5.7)	0(0.0)
Brady	Low	Submerged	F	BLS-F	1	0	0(0.0)	0(0.0)	0(0.0)	3(9.6)	10(32.1)
Brady	Low	Submerged	I	BLS-I	1	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	5(39.4)
Brady	Low	Submerged	J	BLS-J	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	9(23.1)

Phylum	Annelida	Annelida	Annelida	Annelida	Annelida	Arthropoda	Arthropoda	Arthropoda	Arthropoda
Sample	Oligochaeta	Nereidae	Syllidae	Sabellidae *	Ostracoda	Harpacticoida	Calanoida	Naupliar larvae	Caprellidea
BHE-A	0(0.0)	17(27.0)	0(0.0)	0(0.0)	0(0.0)	37(58.8)	0(0.0)	0(0.0)	0(0.0)
BHE-B	20(15.0)	19(14.2)	13(9.7)	0(0.0)	5(3.7)	204(152.7)	0(0.0)	3(2.2)	1(0.7)
BHE-F	0(0.0)	18(26.7)	7(10.4)	0(0.0)	2(3.0)	37(54.8)	0(0.0)	28(41.5)	0(0.0)
BHE-G	0(0.0)	20(21.3)	6(6.4)	0(0.0)	0(0.0)	52(55.3)	0(0.0)	0(0.0)	0(0.0)
BHE-H	0(0.0)	25(22.3)	0(0.0)	0(0.0)	1(0.9)	30(26.7)	0(0.0)	8(7.1)	0(0.0)
BHS-A	0(0.0)	7(30.7)	2(8.8)	0(0.0)	0(0.0)	9(39.5)	0(0.0)	1(4.4)	0(0.0)
BHS-B	2(3.7)	6(11.1)	2(3.7)	0(0.0)	0(0.0)	10(18.5)	0(0.0)	0(0.0)	0(0.0)
BHS-D	2(4.8)	1(2.4)	0(0.0)	0(0.0)	2(4.8)	52(123.8)	0(0.0)	10(23.8)	0(0.0)
BHS-I	0(0.0)	3(4.3)	8(11.6)	0(0.0)	2(2.9)	59(85.5)	0(0.0)	22(31.9)	0(0.0)
BHS-J	0(0.0)	2(4.1)	2(4.1)	0(0.0)	0(0.0)	36(73.9)	0(0.0)	12(24.6)	0(0.0)
BLE-B	1(1.9)	8(15.2)	0(0.0)	0(0.0)	0(0.0)	19(36.2)	0(0.0)	9(17.1)	0(0.0)
BLE-D	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	15(53.0)	0(0.0)	7(24.7)	0(0.0)
BLE-G	0(0.0)	10(11.7)	3(3.5)	0(0.0)	3(3.5)	27(31.5)	0(0.0)	0(0.0)	0(0.0)
BLE-H	1(2.8)	4(11.1)	1(2.8)	0(0.0)	0(0.0)	16(44.4)	0(0.0)	12(33.3)	0(0.0)
BLE-J	1(1.8)	8(14.1)	0(0.0)	0(0.0)	0(0.0)	1(1.8)	0(0.0)	0(0.0)	0(0.0)
BLS-A	0(0.0)	4(17.9)	2(9.0)	0(0.0)	1(4.5)	14(62.8)	0(0.0)	0(0.0)	0(0.0)
BLS-B	0(0.0)	2(11.5)	0(0.0)	0(0.0)	0(0.0)	9(51.7)	0(0.0)	0(0.0)	0(0.0)
BLS-F	0(0.0)	1(3.2)	2(6.4)	0(0.0)	1(3.2)	12(38.5)	0(0.0)	2(6.4)	0(0.0)
BLS-I	0(0.0)	2(15.7)	3(23.6)	0(0.0)	1(7.9)	6(47.2)	0(0.0)	3(23.6)	11(86.6)
BLS-J	0(0.0)	6(15.4)	13(33.4)	0(0.0)	1(2.6)	26(66.8)	0(0.0)	19(48.8)	0(0.0)

Phylum	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Nematoda	
Sample	Gammaridea	Idoteidae *	Sphaeromantidae	Janiridae	Munnidae *	Halicaridae	Chironomid	Nematode	Individuals per sample
BHE-A	2(3.2)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	4(6.4)	0(0.0)	2062(3278.2)§	2136(3397.5)
BHE-B	7(5.2)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	156(116.8)	1(0.7)	372(278.4)	948(709.6)
BHE-F	1(1.5)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	5(7.4)	0(0.0)	596(883.0)§	701(1038.5)
BHE-G	1(1.1)	0(0.0)	1(1.1)	0(0.0)	0(0.0)	7(7.4)	1(1.1)	259(275.5)	399(424.5)
BHE-H	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	3(2.7)	0(0.0)	1238(1102.4)§	1313(1169.2)
BHS-A	4(17.5)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	27(118.4)	3(13.2)	225(986.8)	291(1276.3)
BHS-B	23(42.4)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	42(77.5)	0(0.0)	165(304.4)	265(488.9)
BHS-D	0(0.0)	0(0.0)	1(2.4)	0(0.0)	0(0.0)	47(111.9)	1(2.4)	116(276.2)	252(600.0)
BHS-I	0(0.0)	0(0.0)	1(1.4)	0(0.0)	0(0.0)	30(43.5)	0(0.0)	126(182.6)	274(397.1)
BHS-J	1(2.1)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(2.1)	0(0.0)	200(410.7)	263(542.1)
BLE-B	1(1.9)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(1.9)	2(3.8)	516(982.9)§	559(1064.8)
BLE-D	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	2(7.1)	0(0.0)	115(406.4)	140(494.7)
BLE-G	1(1.2)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	14(16.3)	0(0.0)	48(55.9)	119(138.7)
BLE-H	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	5(13.9)	0(0.0)	34(94.4)	79(219.4)
BLE-J	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	16(28.1)	29(51.0)
BLS-A	2(9.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	4(17.9)	0(0.0)	160(717.5)	200(896.9)
BLS-B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	3(17.2)	0(0.0)	25(143.7)	41(241.4)
BLS-F	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	3(9.6)	0(0.0)	42(134.6)	79(253.2)
BLS-I	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	5(39.4)	0(0.0)	15(118.1)	55(433.1)
BLS-J	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	4(10.3)	0(0.0)	57(146.5)	137(352.2)

Phylum		Rhodophyta	Rhodophyta	Ectoprocta	Ectoprocta	Ectoprocta	
Sample	Taxon Richness	Weight of Corallinacea (g)	Dominant species of Corallinacea in sample	Weight of Flustrellidra (g)	Weight of calcified bryozoa (g)	Weight of Filicrisia (g)	Total weight
BHE-A	7(12.7)	0.629	*Corallina vancouveriensis*	0	0.0009	0	0.6299
BHE-B	16(12.0)	1.336	*C. vancouveriensis*	0	0.024	0	1.36
BHE-F	10(14.8)	0.675	*C. vancouveriensis*	0	0.002	0	0.677
BHE-G	14(14.9)	0.94	*C. vancouveriensis*	0.0009	0.006	0	0.9469
BHE-H	10(8.9)	1.123	*C. vancouveriensis*	0.0009	0.001	0	1.1249
BHS-A	11(48.2)	0.228	*C. vancouveriensis*	0	0.0009	0	0.2289
BHS-B	9(16.6)	0.542	*C. vancouveriensis*	0	0.0009	0	0.5429
BHS-D	13(31.0)	0.42	*C. vancouveriensis*	0	0.0009	0.0009	0.4218
BHS-I	12(17.4)	0.69	*C. vancouveriensis*	0	0.0009	0.0009	0.6918
BHS-J	10(22.6)	0.487	*Bossiella* spp.	0	0.017	0	0.504
BLE-B	10(19.0)	0.525	*C. vancouveriensis*	0	0.0009	0	0.5259
BLE-D	5(17.7)	0.283	*C. vancouveriensis*	0	0	0	0.283
BLE-G	13(15.2)	0.858	*Bossiella* spp.	0.0009	0.016	0	0.8749
BLE-H	9(25.0)	0.36	*C. vancouveriensis*	0.005	0	0	0.365
BLE-J	7(12.3)	0.569	*C. vancouveriensis*	0.002	0	0	0.571
BLS-A	9(40.4)	0.223	*C. vancouveriensis*	0	0	0	0.223
BLS-B	6(40.2)	0.174	*C. vancouveriensis*	0	0	0	0.174
BLS-F	12(38.5)	0.312	*C. vancouveriensis*	0.0009	0.0009	0	0.3138
BLS-I	13(102.4)	0.127	*Bossiella* spp.	0.002	0.0009	0.001	0.1309
BLS-J	10(25.7)	0.389	*Bossiella* spp.	0.0009	0.008	0	0.3979

Appendix 4: : Taxon counts for intertidal site Scott's Bay. Values in brackets are values standardized for dry algal weight. ^ indicates sampling for presence/absence. * indicates organisms not included in statistical analyses because of too few occurrences.

				Phylum	Porifera	Cnidaria	Nemertea	Mollusca	Mollusca	Mollusca	Mollusca
Site	Transect	Exposure	Replicate	Sample	Porifera^	Hydroida^	Nemertea	Polyplacophora	Larvae of gastropoda	Gastropoda	Bivalvia
Scotts	High	Exposed	A	SHE-A	0	1	0(0.0)	0(0.0)	0(0.0)	1(1.0)	60(58.1)
Scotts	High	Exposed	C	SHE-C	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	29(62.4)
Scotts	High	Exposed	E	SHE-E	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	8(12.3)
Scotts	High	Exposed	G	SHE-G	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	5(8.5)
Scotts	High	Exposed	J	SHE-J	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
Scotts	High	Submerged	A	SHS-A	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	9(13.8)
Scotts	High	Submerged	B	SHS-B	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	6(15.8)
Scotts	High	Submerged	C	SHS-C	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	58(152.6)
Scotts	High	Submerged	H	SHS-H	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(3.4)
Scotts	High	Submerged	I	SHS-I	0	1	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
Scotts	Low	Exposed	B	SLE-B	0	1	0(0.0)	0(0.0)	0(0.0)	0(0.0)	9(14.2)
Scotts	Low	Exposed	C	SLE-C	0	1	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(2.6)
Scotts	Low	Exposed	D	SLE-D	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	3(5.4)
Scotts	Low	Exposed	E	SLE-E	0	0	2(3.2)	0(0.0)	0(0.0)	0(0.0)	6(9.7)
Scotts	Low	Exposed	F	SLE-F	0	1	0(0.0)	0(0.0)	0(0.0)	0(0.0)	27(50.4)
Scotts	Low	Submerged	A	SLS-A	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	8(15.4)
Scotts	Low	Submerged	B	SLS-B	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	6(50.4)
Scotts	Low	Submerged	D	SLS-D	0	0	1(0.6)	1(0.6)	21(12.8)	19(11.5)	130(79.0)
Scotts	Low	Submerged	H	SLS-H	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
Scotts	Low	Submerged	J	SLS-J	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	10(33.4)

Phylum	Annelida	Annelida	Annelida	Annelida	Annelida	Arthropoda	Arthropoda	Arthropoda	Arthropoda
Sample	Oligochaeta	Nereidae	Syllidae	Sabellidae *	Ostracoda	Harpacticoida	Calanoida	Naupliar larvae	Caprellidae
SHE-A	3(2.9)	19(18.4)	6(5.8)	0(0.0)	0(0.0)	36(34.8)	0(0.0)	9(8.7)	1(1.0)
SHE-C	0(0.0)	12(25.8)	6(12.9)	0(0.0)	0(0.0)	18(38.7)	0(0.0)	2(4.3)	0(0.0)
SHE-E	0(0.0)	27(41.5)	2(3.1)	0(0.0)	0(0.0)	9(13.8)	0(0.0)	5(7.7)	0(0.0)
SHE-G	0(0.0)	12(20.5)	2(3.4)	0(0.0)	0(0.0)	11(18.8)	0(0.0)	9(15.4)	0(0.0)
SHE-J	1(2.2)	2(4.5)	1(2.2)	0(0.0)	0(0.0)	14(31.4)	0(0.0)	0(0.0)	0(0.0)
SHS-A	0(0.0)	9(13.8)	0(0.0)	0(0.0)	0(0.0)	10(15.3)	0(0.0)	0(0.0)	0(0.0)
SHS-B	0(0.0)	7(18.4)	1(2.6)	0(0.0)	1(2.6)	36(94.7)	0(0.0)	0(0.0)	0(0.0)
SHS-C	0(0.0)	3(7.9)	2(5.3)	0(0.0)	0(0.0)	12(31.6)	0(0.0)	0(0.0)	0(0.0)
SHS-H	0(0.0)	1(3.4)	0(0.0)	0(0.0)	0(0.0)	6(20.6)	1(3.4)	1(3.4)	0(0.0)
SHS-I	0(0.0)	3(5.8)	0(0.0)	0(0.0)	0(0.0)	12(23.3)	0(0.0)	7(13.6)	0(0.0)
SLE-B	1(1.6)	1(1.6)	4(6.3)	0(0.0)	1(1.6)	14(22.0)	0(0.0)	4(6.3)	0(0.0)
SLE-C	0(0.0)	9(23.3)	0(0.0)	0(0.0)	0(0.0)	10(25.9)	0(0.0)	4(10.4)	1(2.6)
SLE-D	0(0.0)	3(5.4)	0(0.0)	0(0.0)	0(0.0)	15(26.8)	0(0.0)	12(21.5)	0(0.0)
SLE-E	0(0.0)	11(17.8)	5(8.1)	0(0.0)	0(0.0)	11(17.8)	0(0.0)	17(27.5)	0(0.0)
SLE-F	0(0.0)	31(57.8)	11(20.5)	0(0.0)	1(1.9)	29(54.1)	0(0.0)	5(9.5)	2(3.7)
SLS-A	0(0.0)	11(21.1)	0(0.0)	0(0.0)	1(1.9)	6(11.5)	0(0.0)	2(3.8)	0(0.0)
SLS-B	0(0.0)	0(0.0)	1(8.40	0(0.0)	0(0.0)	7(58.8)	0(0.0)	0(0.0)	3(25.2)
SLS-D	56(34.0)	14(8,5)	55(33.4)	1(0.6)	7(4.3)	84(51.0)	1(0.6)	0(0.0)	6(3.6)
SLS-H	0(0.0)	1(4.8)	2(9.7)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(4.8)
SLS-J	0(0.0)	6(20.1)	3(10.0)	0(0.0)	1(3.3)	18(60.2)	0(0.0)	8(26.8)	1(3.3)

Phylum	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Nematoda	
Sample	Idoteidae *	Sphaeromatidae	Janiridae	Munnidae *	Halicarid Mites	Chironomid	Nematode	Individuals per sample
SHE-A	0(0.0)	1(1.0)	0(0.0)	0(0.0)	15(14.5)	0(0.0)	161(155.9)	314(304.0)
SHE-C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	27(58.1)	0(0.0)	85(182.80	181(389.2)
SHE-E	0(0.0)	0(0.0)	0(0.0)	0(0.0)	2(3.1)	0(0.0)	56(86.2)	114(175.4)
SHE-G	0(0.0)	1(1.7)	0(0.0)	0(0.0)	5(8.5)	0(0.0)	198(338.5)	244(417.1)
SHE-J	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	60(134.5)	79(177.1)
SHS-A	0(0.0)	1(1.5)	0(0.0)	0(0.0)	3(4.6)	0(0.0)	34(52.1)	67(104.3)
SHS-B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	10(26.3)	0(0.0)	65(171.1)	126(331.6)
SHS-C	0(0.0)	0(0.0)	4(10.5)	0(0.0)	8(21.1)	0(0.0)	40(105.3)	145(381.6)
SHS-H	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(3.4)	0(0.0)	64(219.9)	77(264.6)
SHS-I	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	20(38.9)	43(83.7)
SLE-B	0(0.0)	0(0.0)	0(0.0)	1(1.6)	6(9.4)	0(0.0)	6(9.4)	50(78.7)
SLE-C	0(0.0)	0(0.0)	0(0.0)	0(0.0)	4(10.4)	0(0.0)	15(38.9)	47(119.2)
SLE-D	0(0.0)	0(0.0)	0(0.0)	0(0.0)	3(5.4)	0(0.0)	59(105.5)	99(177.1)
SLE-E	1(1.6)	0(0.0)	0(0.0)	0(0.0)	2(3.2)	0(0.0)	63(101.8)	121(195.5)
SLE-F	0(0.0)	0(0.0)	0(0.0)	0(0.0)	14(26.1)	1(1.9)	295(550.4(	420(783.6)
SLS-A	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	70(134.4)	102(195.8)
SLS-B	0(0.0)	0(0.0)	0(0.0)	0(0.0)	4(33.6)	0(0.0)	15(126.1)	37(310.9)
SLS-D	0(0.0)	0(0.0)	3(1.8)	3(1.8)	101(61.4)	0(0.0)	234(142.2)	744(452.0)
SLS-H	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	4(19.3)	10(48.3)
SLS-J	0(0.0)	0(0.0)	0(0.0)	0(0.0)	5(16.7)	0(0.0)	56(187.3)	111(371.2)

Phylum		Rhodophyta	Rhodophyta	Ectoprocta	Ectoprocta	Ectoprocta	
Sample	Taxon Richness	Weight of Corallinacea (g)	Dominant species of Corallinacea in sample	Weight of *Flustrellidra* (g)	Weight of calcified bryozoa (g)	Weight of *Filicrisia* (g)	Total weight
SHE-A	13(12.6)	1.033	*Corallina vancouveriensis*	0	0.0009	0	1.0339
SHE-C	9(19.4)	0.465	*C. vancouveriensis*	0	0.0009	0	0.4659
SHE-E	9(13.8)	0.65	*C. vancouveriensis*	0	0.0009	0	0.6509
SHE-G	9(15.4)	0.585	*C. vancouveriensis*	0	0.0009	0	0.5859
SHE-J	6(13.5)	0.446	*C. vancouveriensis*	0	0.0009	0	0.4469
SHS-A	7(12.3)	0.652	*C. vancouveriensis*	0	0.0009	0	0.6529
SHS-B	7(18.4)	0.38	*C. vancouveriensis*	0	0	0	0.38
SHS-C	9(23.7)	0.38	*C. vancouveriensis*	0	0.111	0	0.491
SHS-H	9(30.9)	0.291	*C. vancouveriensis*	0	0.0009	0	0.2919
SHS-I	5(9.7)	0.514	*Bossiella* spp.	0	0	0	0.514
SLE-B	13(20.5)	0.635	*C. vancouveriensis*	0	0.001	0.0009	0.6369
SLE-C	10(23.3)	0.386	*C. vancouveriensis*	0.0009	0.0009	0	0.3878
SLE-D	9(16.1)	0.559	*Bossiella* spp.	0.0009	0.0009	0	0.5608
SLE-E	12(19.4)	0.619	*C. vancouveriensis*	0.0009	0.0009	0	0.6208
SLE-F	14(26.1)	0.536	*C. vancouveriensis*	0.0009	0.0009	0.0009	0.5387
SLS-A	9(17.3)	0.521	*C. vancouveriensis*	0.003	0.0009	0	0.5249
SLS-B	7(58.8)	0.119	*C. vancouveriensis*	0.017	0	0.0009	0.1369
SLS-D	21(12.8)	1.646	*C. vancouveriensis*	0.003	0.0009	0.0009	1.6508
SLS-H	6(29.0)	0.207	*Bossiella* spp.	0.0009	0	0	0.2079
SLS-J	12(40.1)	0.299	*Bossiella* spp.	0.044	0.0009	0	0.3439

Appendix 5: Results of 2-way MANOVA for comparison of the two variables: height and exposure from intertidal data. Asterisk indicates significance at level of $p<0.05$.

		Halacaridae		Caprellidea		Bivalvia		Nereidae		Syllidae		Ostracoda		Gastropoda	
	df	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Height	1	464.2	0.517	288.6	2.259	694.7	0.732	136.8	1.230	192.1	3.656	22.7	6.805*	42.1	2.615
Exposure	1	877.0	0.977	215.0	1.682	409.2	0.431	2360.0	21.224*	120.8	2.299	0.911	0.273	0.546	0.034
HXE	1	663.5	0.739	244.6	1.914	12.8	0.013	406.3	3.654	192.8	3.671	4.527	1.359	1.500	0.093
Residual	56	897.3		127.8		948.9		111.2		52.5		3.3		16.1	

		Larvae of gastropoda		Harpacticoida		Gammaridea		Sphaeromatidae		Janiridae		Nemertea	
	df	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Height	1	47.4	4.298*	476.5	0.403	162.3	2.485	2.172	4.223*	1.581	0.24	0.595	1.474
Exposure	1	4.5	0.405	1897.5	1.606	104.4	1.570	0.5	1.004	2.1	1.111	2.0	5.001*
HXE	1	9.2	0.839	594.4	0.503	110.9	1.667	0.008	0.015	0.98	0.510	0.977	2.421
Residual	56	11.0		1181.2		66.5		0.5		1.9		0.404	

		Chironomid		Polyplacophora		Naupliar larvae		Oligochaeta		Calanoida		Nematoda (log 10)	
	df	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Height	1	4.9	1.44	0.3	1.219	60.8	0.173	3.9	0.164	0.4	1.617	1.6	7.206*
Exposure	1	0.2	0.065	0.002	0.007	482.4	1.377	4.3	0.183	0.7	2.468	1.0	4.826*
HXE	1	8.5	2.512	0.035	0.125	1154.7	3.295	26.0	1.094	0.4	1.617	0.5	2.321
Residual	56	3.4		0.28		350.4		23.7		0.274		0.216	

	Value	F	Error df	Sig.
Height	1.025	1.896	37	0.045*
Exposure	1.132	2.095	37	0.025*
Height X Exposure	0.734	1.358	37	0.206